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Ecology of a Vulnerable Shorebird across a Gradient of Habitat Alteration: Bristle-Thighed Curlews (*Numenius tahitiensis*) (Aves: Charadriiformes) on Palmyra Atoll[1]

Ana Sofía Guerra,[2,4] *Fiorenza Micheli,*[2] *and Chelsea L. Wood*[2,3]

Abstract: Palmyra Atoll, USA, in the Central Pacific, has remained mostly uninhabited since construction and abandonment of a U.S. naval base during World War II. However, the effects of Navy modifications have persisted, affecting physical conditions and benthic habitat quality of Palmyra's lagoon sand flats. Sand flats provide important nonbreeding habitat for Bristle-thighed Curlews (*Numenius tahitiensis*), a migratory shorebird listed as "vulnerable" by the International Union for Conservation of Nature and Natural Resources. We used camera trapping, observations of focal individuals, and quantification of prey availability and sediment characteristics to assess curlew habitat use across different levels of historical anthropogenic impact. Habitat preferences were not determined by the degree of land reclamation impact on lagoon flat habitat, although the two most preferred sites were both highly impacted. Curlew abundance was most strongly correlated with availability of prey items, such as spionid polychaetes (*Malacoceros* sp.). Our findings provide new ecological information on a shorebird species that is rarely studied and provides useful information for habitat management at Palmyra Atoll and other curlew wintering grounds.

Historical accounts of remote Pacific Islands evoke landscapes, flora, and fauna profoundly different from those observed today (Dawson 1959, Stoddart 1968). Twentieth-century visitors to these islands introduced alien species, dredged reefs to create boat channels, expanded land masses to construct runways, and left behind debris from wrecked vessels (Magier and Morgan 2012). In one of the first scientific assessments of anthropogenic impacts on a coral reef ecosystem, Dawson (1959) documented the dramatic modifications to the lagoons and vegetation of Palmyra Atoll, USA, that accompanied the construction and abandonment of a World War II–era U.S. naval base. Although the island has remained mostly uninhabited since the abandonment of the base in 1945, the effects of these past alterations persist to the present day (Maragos, Friedlander, et al. 2008).

Today, Palmyra Atoll provides an important habitat for several species of resident nesting seabirds and at least four species of migratory shorebirds, three of which are of conservation concern (Engilis and Naughton 2004; Maragos, Miller, et al. 2008). Shorebirds inhabit beaches, grasslands, wetlands, and tundra (Brown et al. 2001; Warnock, Elphick, and Rubega 2001; Colwell 2010)—habitats that are rapidly disappearing due to coastal and agricultural development and pollution (Noss, LaRoe, and Scott 1995; Junk 2002). Recent evidence suggests that global shorebird populations are in decline (Colwell 2010).

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Bristle-thighed Curlews (*Numenius tahitiensis*) are shorebirds that breed in Alaska in the boreal summer and winter on small tropical and subtropical oceanic islands (Kessel 1989, Gill and Redmond 1992, Marks et al. 2002). They are the only species of shorebird that depends exclusively on oceanic islands for feeding during the nonbreeding season (Kessel 1989, Gill and Redmond 1992). The International Union for Conservation of Nature and Natural Resources, IUCN, Red List (BirdLife International 2008) classifies this species as "vulnerable" due to its small and declining populations. Declines are driven by predation on curlews on their wintering grounds by introduced mammals (Gill and Redmond 1992, Marks 1993) as well as by loss of these wintering grounds to land development (Wodzicki 1981, BirdLife International 2008).

While there is substantial information about *N. tahitiensis* from its breeding grounds in Alaska (Gill et al. 1990, Lanctot et al. 1992, Marks et al. 2002), information on habitat use at nonbreeding sites is scarce and generally obtained from large-scale bird surveys (Gill and Redmond 1992, Marks and Redmond 1994). Wintering curlews appear to have varied, generalized diets that range from terrestrial insects and bird eggs to fiddler crabs and other intertidal invertebrates (Bakus 1967, Ely and Clapp 1973, Gill and Redmond 1992, Marks and Hall 1992). In a study conducted on Rangiroa Atoll (Tuamotu Archipelago), curlews were found mostly in saltpan habitats and channels between islets, and, less often, on ocean terraces and sand beaches (Gill and Redmond 1992). Gill and Redmond (1992) suggested that the presence of humans and introduced domesticated and feral animals, not habitat type, might be the most important determinant of curlew distributions on Rangiroa Atoll and in other areas where they have been historically hunted or are at risk of predation.

In addition to being a location of critical importance for Bristle-thighed Curlews (Marks and Redmond 1994), Palmyra offers a unique opportunity to compare habitats with dramatically different histories of human disturbance within a single atoll. Palmyra Atoll hosts one of the largest aggregations of curlews of any Central Pacific Island, with 266 individuals as of 2010 (U.S. Fish and Wildlife Service 2011). Shallow, nonvegetated, intertidal sand and mud flats occupy the margins of Palmyra Atoll's lagoons. Bristle-thighed Curlews forage on these flats during low tides and congregate on the atoll's only airplane runway at high tides (A. S. Guerra, pers. obs.). Palmyra Atoll has been largely uninhabited throughout its history, but the effects of human occupation during World War II persist to the present day (Collen, Garton, and Gardner 2009). In the 1930s and 1940s, the U.S. Navy dramatically modified the atoll, cutting a channel through the reef, nearly doubling the total land area of the islets through land reclamation, and restricting water flow to parts of the atoll's inner lagoon and flats by building roads and causeways between them (Collen, Garton, and Gardner 2009). The modifications altered natural water flow and increased lagoon water retention and temperatures, which affect sediment particle size and duration of the flat's submersion during high tides, and permanently lowered water levels in the lagoon, which increased the extent of shallow lagoon flats accessible to intertidal foragers (Maragos, Friedlander, et al. 2008; A. S. Guerra, pers. obs.). This resulted in sand flats with varying levels of impact and differing invertebrate communities along the shores of the lagoon (A. S. Guerra, pers. obs.). In 2010, a plan to restore parts of the atoll to their pre–World War II state by reducing or removing artificial restrictions to water flow through lagoons was proposed to the U.S. Fish and Wildlife Service by the Army Corps of Engineers (A. Pollock, USFWS Palmyra Atoll Refuge Manager, pers. comm.). The corps' proposal was not approved, but such restoration efforts are still being considered, and any restoration aiming to remove artificial water restrictions is likely to substantially change Palmyra's lagoon flats (A. Pollock, USFWS Palmyra Atoll Refuge Manager, pers. comm.). The potential impact of this intervention on shorebirds has not yet been explored.

To examine the potential consequences of past lagoon flats alteration and proposed restoration, we assessed curlew habitat use and feeding behavior across lagoon flat sites with varying degrees of anthropogenic impact due to land modifications. Our goal was to quantify spatial variability in *N. tahitiensis* habitat use on Palmyra Atoll, to elucidate how land alterations made to the atoll by the U.S. Navy during World War II might have affected availability of lagoon flat habitat for curlews, and to shed light on whether planned restoration efforts might increase or decrease habitat availability for curlews. We observed high abundances of fiddler crabs (one of the preferred prey of curlews on other wintering grounds; Bakus 1967, Gill and Redmond 1992) at sites where effects such as water restriction from land reclamation were acute, and we therefore predicted that curlews would prefer these highly impacted sites relative to other flats. Additionally, sediment size can affect abundances and densities of different prey types (Yates et al. 1993) and shorebird foraging behavior (Colwell 2010). Shorebirds with probing behavior tend to favor fine sediment, while shorebirds such as curlews, which peck at the surface of the sediment, favor coarser sediment (Colwell 2010). Thus we predicted that sites with coarser sediments might be preferred.

We quantified Bristle-thighed Curlew presence and abundance across 12 sites varying in land reclamation impact by using camera traps at each of the sites during low tides. We studied foraging behavior and preferences by observing curlew foraging behavior and sampling macroinvertebrates at each site.

METHODS

We conducted fieldwork on the lagoon sand and mud flats of Palmyra Atoll National Wildlife Refuge (5.86° N, 162.08° W), a tropical atoll in the central equatorial Pacific Ocean. All data were collected between 18 July and 20 August 2012.

Site Selection

We selected sites by first delineating impact zones across the entire atoll. Two observers familiar with Palmyra's lagoon flats (A.S.G. and C.L.W.) consulted historical aerial photography (F.A.B. Pearl Harbor 1935*a*), modern satellite imagery (Google Earth V.7.0.3.8542, 2013), and a study of historical geomorphology of the atoll (Collen, Garton, and Gardner 2009) to delineate zones of high, moderate, and no land-reclamation impact. Criteria for these categories included the site's proximity to reclaimed land, difference in land area before and after construction, and restrictions to water flow due to construction of the naval base (Maragos, Friedlander, et al. 2008; Collen, Garton, and Gardner 2009) (Figure 1). We then selected a total of 12 sites across impact zones (5 high impact sites, 4 low impact sites, and 3 no impact or control sites). We selected sites that were composed entirely of sand or mud flat, remained mostly exposed during the two daily low tides, and were accessible to observers (Figure 2).

Prey Abundance

To measure the relative availability of potential curlew prey items, we sampled macroinvertebrates using a 20 cm diameter sediment core. We selected coring sites by randomly choosing a cardinal direction (0° to 360° from north) and sampling at a spot 3 m in that direction from the center point of the site (Figure 3). Three cores were taken at each site once during the study period and the cored sediment was passed through a nested mesh sieve of 6 mm and 1 mm mesh size. Macroinvertebrates recovered from the sieve were identified to the lowest taxonomic level possible and counted in the field (Gosliner, Behrens, and Williams 1996; Colin and Arneson 1997; Madrigal 1999; Severns 2001; Hoover 2006). We calculated taxon richness as the number of macroinvertebrate species present at each site and prey abundance as the average abundance of macroinvertebrates at each site.

Because fiddler crabs (*Uca tetragonum*) were not adequately characterized by our sediment core due to their rapid burrowing behavior, we obtained an estimate of relative fiddler crab abundance by having two observers (A.S.G. and C.L.W.) visually estimate percentage cover of fiddler crab-inhabited sand flat, distinctive because the crabs form dense colonies of burrows (A. S. Guerra, pers. obs.). Each observer

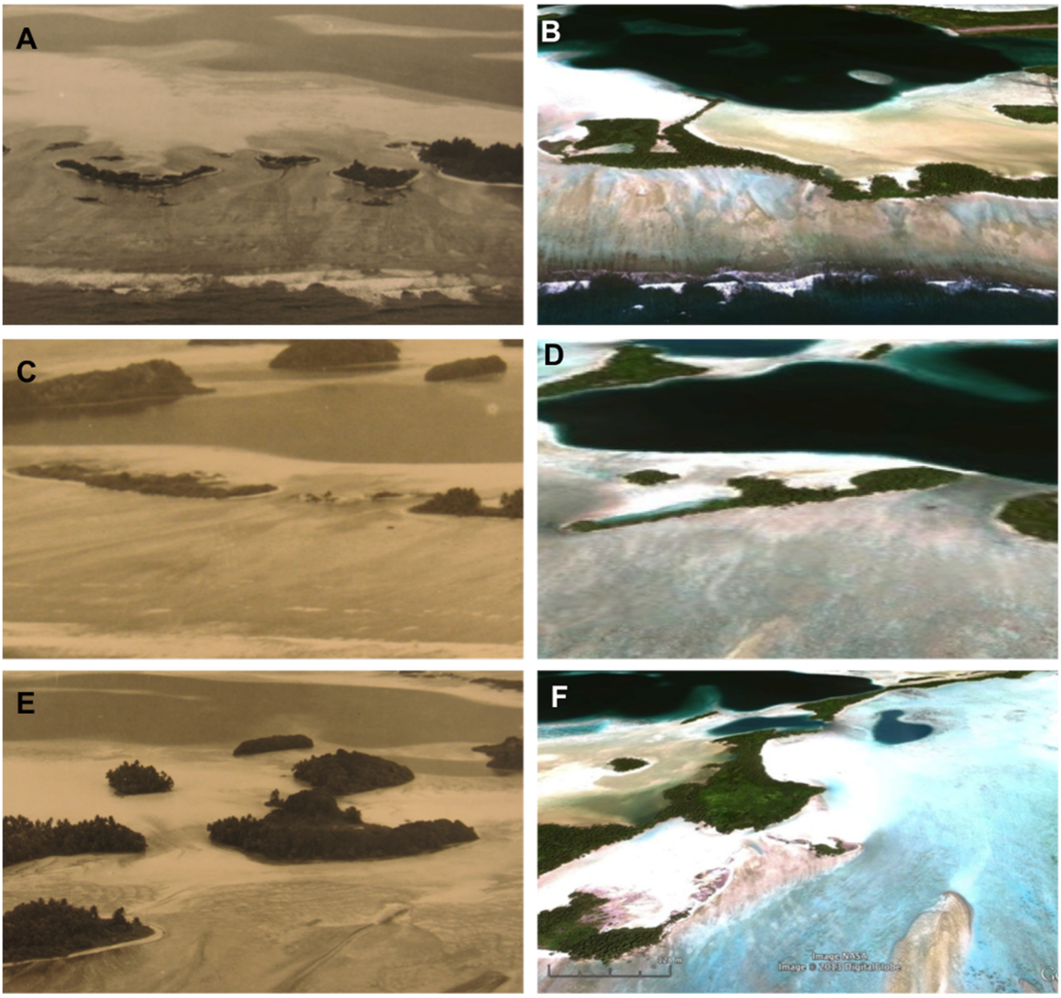

Figure 1. General aspect of lagoon flat habitats prior to the construction of the U.S. naval base (*left* column) and general aspect of the lagoon flat habitats in 2009 (*right* column) at a high impact site (HI3 and HI2; *A*, *B*), low impact site (*C*, *D*), and no impact site (NI1; *E*, *F*). Photo: F.A.B. Pearl Harbor (1935*b*, *c*), Google Earth V.7.0.3.8542, 2013.

made an independent estimate of the extent of fiddler crab habitat at each site, and we used the average of these two estimates, which were strongly correlated ($R^2 = 0.95$, df = 10, $P < .001$), as a metric for relative fiddler crab abundance among sites.

Sediment

To quantify sediment characteristics, we measured sediment grain size at each site using a 4 cm diameter, 10 cm long sediment core. We took three sediment cores from each site, using the same methodology as used for selecting invertebrate coring sites. In the laboratory, we passed these sediment samples through three nested sieves (1 mm, 500 μm, and 100 μm) and then dried samples in a drying oven. We then measured the dry weight of the material retained in each sieve to calculate the ratio of large (>1 mm) to small (<100 μm) sediment grain mass.

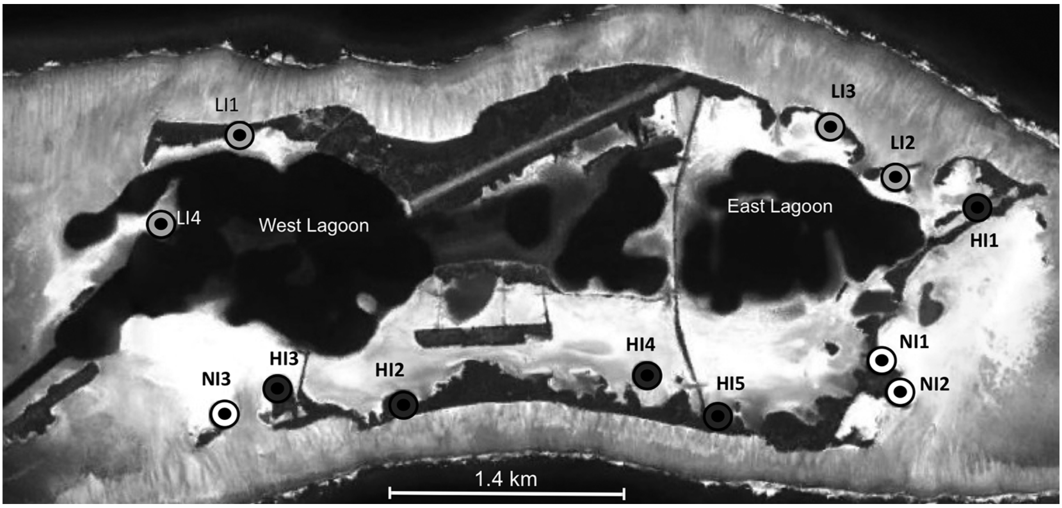

Figure 2. Map of Palmyra Atoll showing 12 study sites named after their determined level of impact: high impact (HI) in dark gray, low impact (LI) in light gray, and no impact/control (NI) in white.

Camera Trapping

We used time-lapse photography to count birds on the flats during low tide. Camera trapping offers several advantages over direct observation: it limits observer bias, provides an objective record, increases the extent of area that can be simultaneously sampled, and is less likely to influence animal behavior than in situ observations by researchers (Cutler and Swann 1999; Silveira, Jácomo, and Diniz-Filho 2003; O'Brien and Kinnaird 2008). At each of our 12 sites, we placed time-lapse wildlife cameras (Covert Extreme Black 60 Trail Camera, DLC, Lewisburg, Kentucky) on the demarcated reference area to capture images of the lagoon flat and any birds present during low tides. Trail cameras were attached to a post in a location where the devices would not be submerged or splashed, and they were therefore placed on the shoreline, at the average level of water at high tide. This results in bias against sighting curlews near the shoreline, a limitation that must be borne in mind when interpreting results. The far boundary of each site was set at 50 m into the lagoon from the high tide line, the approximate maximum distance at which our cameras (placed at the high tide line) could provide sufficient resolution to identify a Bristle-thighed Curlew (Figure 3). At each site, we placed reference markers around the boundary of the camera's triangular field of view out to 50 m. These boundaries allowed us to standardize an area of 0.12 ha for each site. Six cameras were deployed and rotated among the sites throughout a five-week study period for an average of 13 ± 3.52 (mean ± SE) monitoring periods per site. Each deployment was ~6.19 ± 2.16 hr long (Table S1 in Supplemental Appendix).

Authors' Note: Supplemental materials available only on BioOne (http://www.BioOne.org/).

We set out cameras at each of our 12 sites during daytime high tides between 18 July and 20 August 2012. Cameras remained deployed for the entirety of the low tide immediately following the high tide camera deployment, capturing curlews visiting that site for the entire time that the site was exposed. We then retrieved and downloaded the cameras at the subsequent daytime high tide. All cameras were programmed to record one still photograph every 30 sec. We scored photos by recording the number and species identity of all birds present within the 0.12 ha reference area

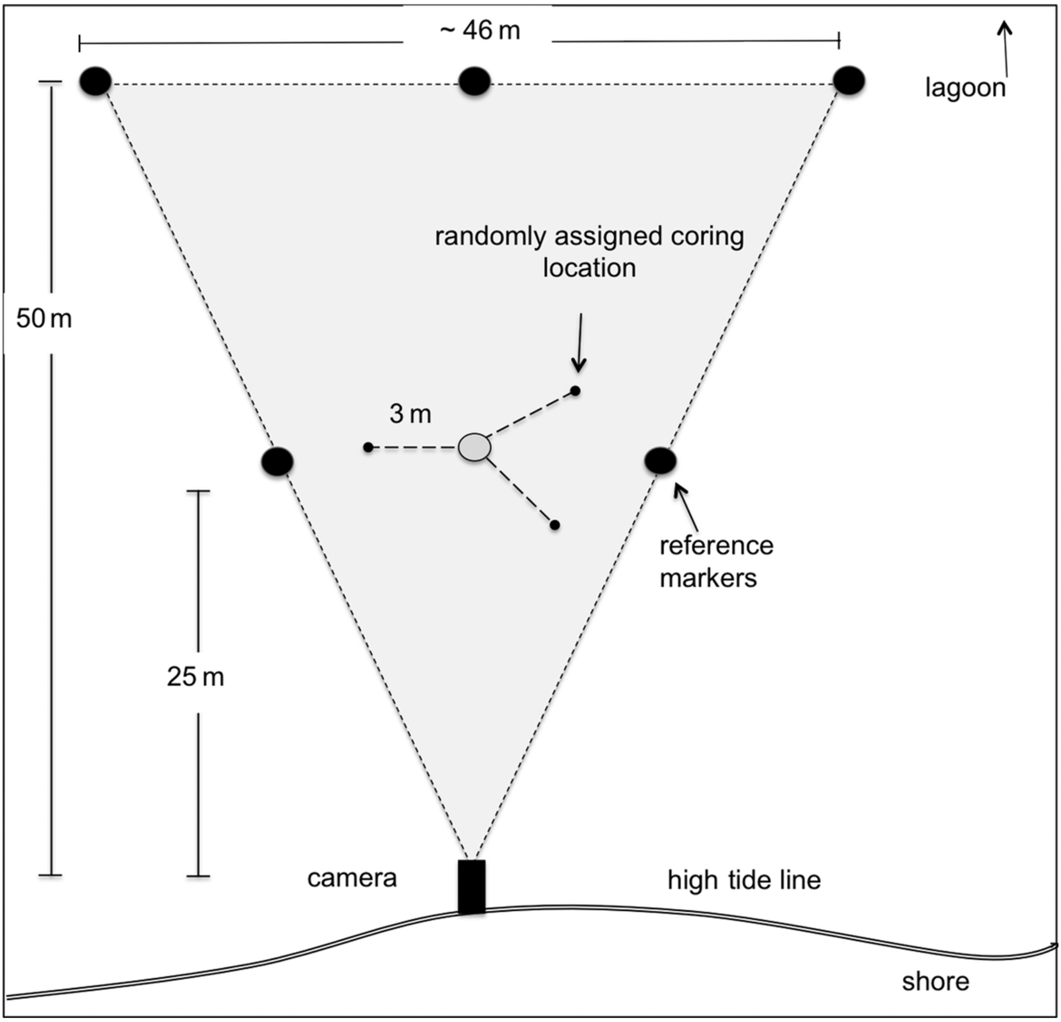

Figure 3. Generalized layout of sites showing placement for camera and reference markers as well as orientation relative to the lagoon and shoreline. An example of three random coring locations within a site is also shown.

throughout the entire low tide. We considered the beginning of the low tide to be the time at which the first mounds of benthic sediment broke the surface of the water at each site; we considered the end of the low tide to be the time when all sediment at the site was entirely covered by water. This technique allowed us to quantify both curlew presence throughout one camera deployment per site and mean bird abundance across photographs (every 30 sec) per low tide per site.

Focal Sampling

To quantify differences in behavior of curlews among sites, we performed direct observations and developed curlew time budgets for each site. During each observation session, we conducted focal observations on five individuals sequentially (Table S2 in Supplemental Appendix). Focal sampling has been used to describe and quantify behavior in a variety of shorebird species (e.g., Burger and Gochfeld

1991; Turpie and Hockey 1993, 1997; Leeman et al. 2001). Each focal individual was observed independently and continuously for up to 10 min. If no Bristle-thighed Curlews were present at the site, we scanned the site for 40 min before terminating an observation session. When *N. tahitiensis* were present, we used 8 × 42 mm binoculars to observe behavior and continuously recorded the focal individual's behavior into a digital voice recorder. Noted behaviors included walking, pecking, eating (swallowing), handling prey, vocalizing, preening, standing, and flying. If a focal individual was lost from sight before 10 min elapsed, we noted the duration of the observation to that point. We conducted only one observation per bird during an observation session. When there were not enough curlews present at the site to conduct five observations, we conducted observations on as many curlews as possible without using the same individual more than once.

We analyzed recordings of curlew behavior using quantitative behavioral analysis software (JWatcher 1.0, University of California Los Angeles and Macquarie University, Sydney, 2006) and calculated the proportion of time allocated to each behavior and the number of pecks per minute per focal observation, as well as the proportion of time spent eating at each of the sites. We then used rate of pecking (pecks per minute) and time allocated to eating per observation session per site as a proxy for the availability of foraging opportunities at each site.

Statistical Analysis

We began by comparing environmental characteristics among sites (HI1, HI2, HI3, HI4, HI5, LI1, LI2, LI3, LI4, NI1, NI2, NI3) and impact categories (high, low, and no impact). We used a general linear mixed model for each environmental characteristic of interest: sediment grain size ratio (mass of large sediment grain fraction/mass of small sediment grain fraction) and macroinvertebrate taxon richness. Models included impact category (high, low, and none) as a fixed effect and site as a random effect nested in the impact category. This analysis was conducted using the *lmer* function (package *lme4*) in R, and *P* values were extracted with *pvals.fnc* (*language R* package; *R* 2.14.1 GUI 1.43, R Foundation for Statistical Computing, 2011). We used one-way analysis of variance (ANOVA) to investigate variability of sediment grain size ratio and macroinvertebrate taxon richness among sites. We also used linear mixed models, including site as a random effect, to examine the relationship between macroinvertebrate taxon richness and sediment grain size ratio, and the relationship between the abundance of different macroinvertebrate taxa and sediment grain size ratio (using glmer function [lme4 package in R; R 2.14.1 GUI 1.43, R Foundation for Statistical Computing, 2011], which generates estimate parameters of model using Laplace method approximation).

Curlew abundance was quantified as number of birds per photo and was averaged among all photos within a camera deployment to generate an average number of birds per photo per deployment. There were many camera deployments in which no curlews were detected, resulting in zero-inflated data. To account for this, we broke curlew data down into two parts: curlew presence/absence and curlew abundance where present.

To compare patterns in curlew presence/absence among sites and impact categories, we used a mixed effects logistic regression, with impact category as a fixed effect and site as a random effect (using *glmmPQL* function, *MASS* and *stats* packages in R; R Core Team 2015). To assess whether curlew presence/absence was related to the abundance and diversity of invertebrate prey or by sediment characteristics, we ran similar logistic regressions of curlew presence/absence against macroinvertebrate taxon richness, the abundance of each invertebrate taxon, and sediment grain size ratio.

Then, to compare patterns in curlew abundance where curlews were present (i.e., excluding all camera deployments where curlews were not present), we used general linear mixed models (using *lme* function, *nlme* package in R; R Core Team 2015). The model included the impact category as a fixed effect and site as a random effect nested in impact category. We transformed mean curlew abundance data using a fourth-root transformation to conform to the assumption of homogeneity of variance (after Kirchner 1995, Gelman 2007). To assess whether curlew abundance (excluding camera deployments where curlews were not present) was related to the abundance and diversity of invertebrate prey or to sediment characteristics, we ran linear fixed effects models of curlew abundance (excluding deployments with no curlews) against macroinvertebrate taxon richness, the abundance of each macroinvertebrate taxon, and sediment grain size ratio.

Pecking behavior was quantified as number of pecks per minute observed during focal follows. To account for these zero-inflated data, we broke the pecking rate variable into two variables: pecking behavior present/absent and pecking rate (average number of pecks per minute) for follows in which pecking was observed. To compare patterns in pecking behavior presence/absence among sites and impact categories, we used a mixed effects logistic regression, with the impact category as a fixed effect and site as a random effect (using *glmmPQL* function, *MASS* and *stats* packages in R; R Core Team 2015). To assess whether presence/absence of pecking behavior was related to the abundance and diversity of invertebrate prey or by sediment characteristics, we ran similar logistic regressions of pecking behavior presence/absence against macroinvertebrate taxon richness, the abundance of each invertebrate taxon, and sediment grain size ratio.

For the focal follows in which pecking behavior was present, we used general linear mixed models to compare pecking rate across impact categories (using *lme* function, *nlme* package in R; R Core Team 2015). The model included the impact category as a fixed effect and site as a random effect. Average pecking rate was also regressed against average abundance of *N. tahitiensis* within each site to test whether pecking rates were influenced by bird densities and possible interference among individual birds.

RESULTS

We conducted a total of 156 camera sessions, with an average of 13 sessions per site and 6.2 hr of data per session (Table S1 in Supplemental Appendix). Curlews were absent from 124 of the 156 sessions; they were present between 70% and 75% of the time at sites with highest curlew presence and abundance and absent 100% of the time at sites with lowest curlew presence and abundance. We also conducted a total of 30 observation sessions and 38 focal observations (Table S2 in Supplemental Appendix). On average, across sites where curlews were present, the birds spent 40% of their time walking, 33% standing, 8% pecking, 6% flying, 4% eating, 2% preening, 1% handling prey, and 0.1% vocalizing. Average pecking rate for all focal observations was 4.36 pecks per minute.

Site Characteristics and Foraging Opportunity Differences

There were no significant differences in sediment grain size ratio between the control (no impact) and high impact categories (estimate = 0.42 ± 0.44, df = 34, *t*-value = 0.965, $P = .34$), or between control and low impact categories (estimate = 0.45 ± 0.45, df = 34, *t*-value = 0.971, $P = .34$). However, sediment grain size ratio was significantly different among sites (ANOVA, $F_{11,24} = 9.85$, $P < .001$). A post hoc Tukey comparison showed sediment grain size ratio was significantly larger at sites HI1, HI5, LI1, and LI2 than at the remainder of the sites ($P < .01$) (Figure 4*B*).

Average macroinvertebrate taxon richness for all sites was 5.56 ± 0.56. Macroinvertebrate taxon richness was marginally significantly higher at no impact sites relative to high impact sites (control = 7.22 ± 0.543, high impact = 4.467 ± 0.631; estimate = –2.756 ± 1.262, df = 9, *t*-value = –2.18, $P = .06$), but there was no difference between no impact and low impact sites (low impact = 5.667 ± 0.541, estimate = –1.556 ± 1.320, df = 9, *t*-value = –1.179, $P = .26$). There was also a significant difference in taxon richness among sites (ANOVA, $F_{(11,24)} = 4.13$, $P = .002$). A post hoc Tukey comparison showed that macroinvertebrate taxon richness was significantly greater at sites HI3, NI2, and NI3 than at the remainder of the sites ($P < .05$) (Figure 4*A*). Macroinvertebrate taxon richness and sediment grain size

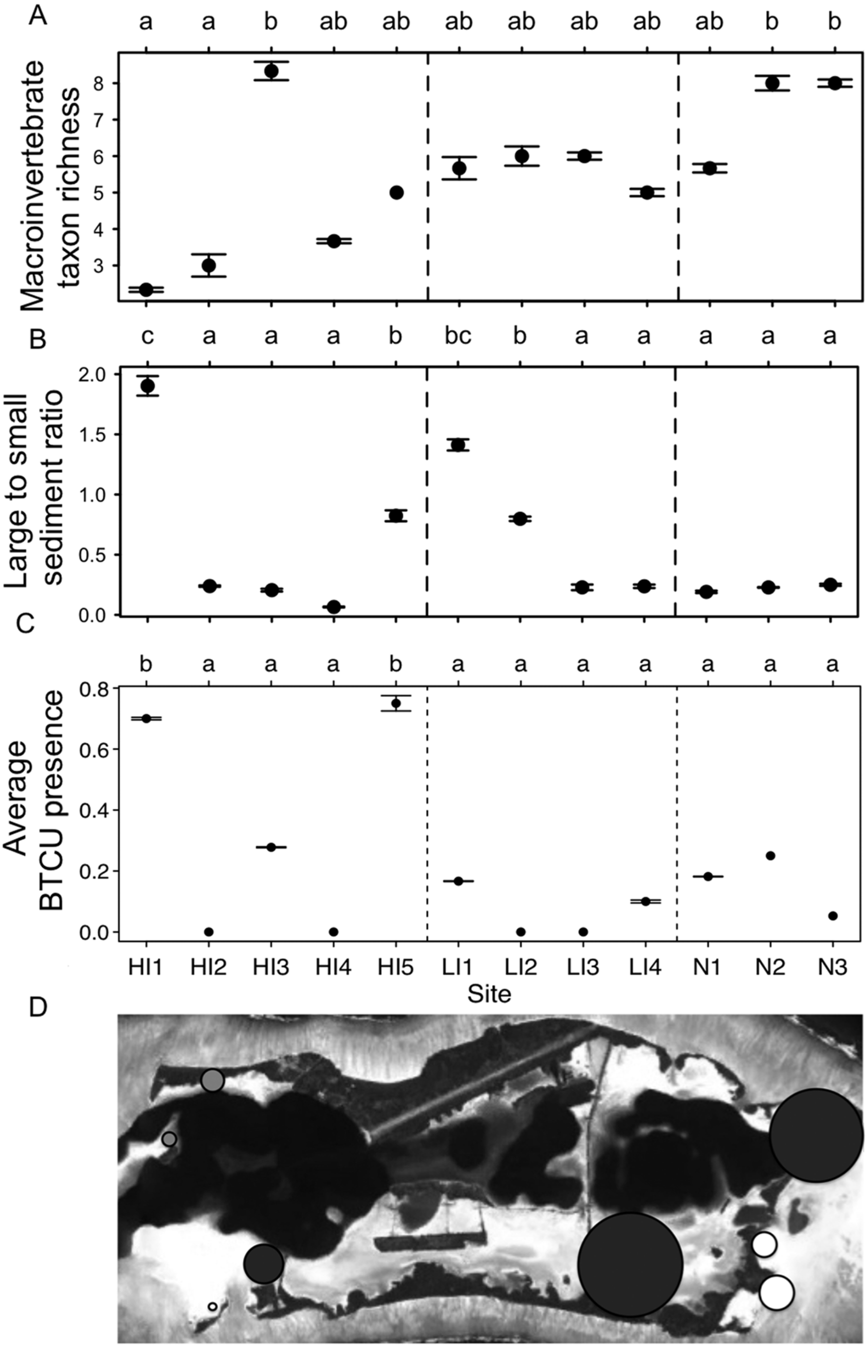

FIGURE 4. (*A*) Macroinvertebrate taxon richness averaged (with 95% confidence interval) within low tide at each site. (*B*) Large to small sediment ratio averaged within low tide at each site. (*C*) Presence of Bristle-thighed Curlews (BTCUs) averaged over all low tides at each site. (*D*) Map shows the relative proportion of the average presence of curlews at sites based on the diameter of the circles. Hues represent level of impact: high impact (dark gray), low impact (light gray), no impact (white).

ratio were not significantly related (estimate = –0.878 ± 0.713, *t*-value = –1.232, df = 23, *P* = .23). Sediment grain size ratio was not related to the abundance of any macroinvertebrate taxon (Table S4 in Supplemental Appendix).

Curlew Presence/Absence and Abundance

Presence/absence of Bristle-thighed Curlews did not differ between control (no impact) and high impact categories (estimate = 0.678 ± 1.188, *t*-value = 0.570, df = 9, *P* = .58), or between control and low impact categories (estimate = –1.101 ± 1.334, *t*-value = –0.825, df = 9, *P* = .43). However, there was a significant difference among sites, with curlew presence significantly more likely at site HI1 (estimate = 2.46 ± 1.04, *z*-value = 2.368, df = 155, *P* = .02) and site HI5 (estimate = 2.71 ± 0.97, *z*-value = 2.803, df = 155, *P* = .005) relative to all other sites (Figure 4*C*). There was no significant relationship between curlew presence/absence and macroinvertebrate taxon richness (estimate = –0.002 ± 0.260, *t*-value = 0.006, df = 10, *P* = .99). Curlew presence was positively related to the abundance of spionid polychaetes (*Malacoceros* sp.), but it was not significantly related to the abundance of any other macroinvertebrate taxon (Figure 5, Table 1). The sediment grain size ratio was positively related, although not significantly so, with curlew presence (estimate = 1.686 ± 0.779, *t*-value = 2.16, df = 10, *P* = .055) (Figure 6).

Using only camera deployments where curlews were present, we found that curlew abundance did not significantly differ between control (control = 0.003 ± 0.0002) and low impact categories (low impact = 0.021 ± 0.001; estimate = 1.27 ± 0.10, *t*-value = 1.208, df = 5, *P* = .28), between low impact and high impact categories (high impact = 0.049 ± 0.009; estimate = 0.03 ± 0.09, *t*-value = 0.292, df = 5, *P* = .78), or between high impact and control categories (estimate = 0.15 ± 0.08, *t*-value = 2.009, df = 5, *P* = .10). We also found no difference in curlew abundance among sites (ANOVA, $F_{(7,24)} = 2.092$, *P* = .08). There was no significant relationship between curlew abundance and macroinvertebrate taxon richness across sites (estimate = –0.021 ± 0.016, df = 6, *t*-value = –1.326, *P* = .23). Curlew abundance was not significantly related to the abundance of any macroinvertebrate taxon (Table S3 in Supplemental Appendix) and there was also no relationship between curlew

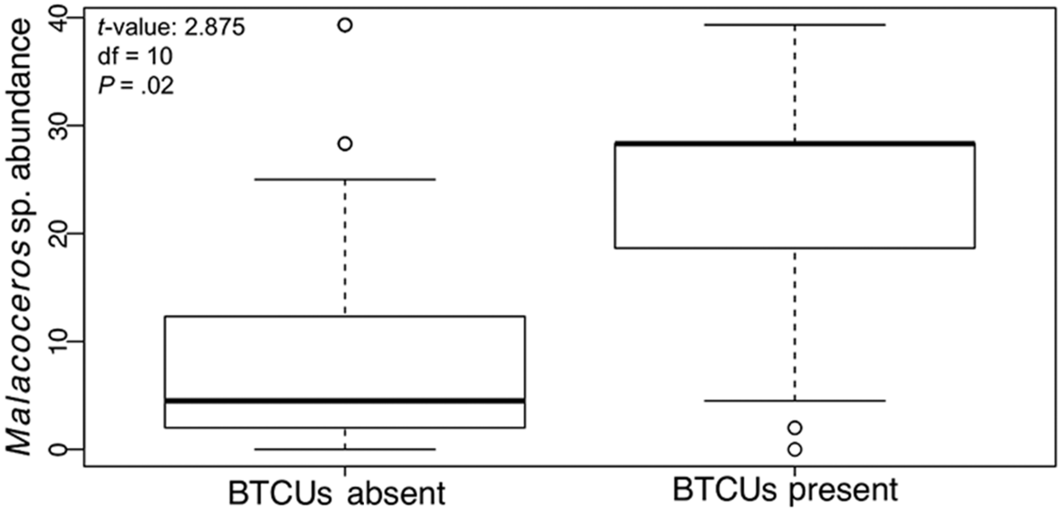

FIGURE 5. Presence of Bristle-thighed Curlews (BTCUs) averaged over all low tides at each site for *Malacoceros* sp. polychaetes.

TABLE 1

Results of General Linear Mixed Model for the Relationship between the Abundance of Various Invertebrate Species and Bristle-thighed Curlew Presence

Invertebrate spp.	Taxonomic Group	Estimate	± SE	*t*-Value	df	*P*
Holothurid sp. 1	Sea cucumber	−0.0047	0.0306	−0.153	10	.88
Polychaete sp. 2	Polychaete	0.0495	0.0832	0.596	10	.57
Polychaete sp. 3	Polychaete	−0.0329	0.0246	−1.340	10	.21
Ptychodera flava	Hemichordate	0.1351	0.1909	0.708	10	.5
Malacoceros sp.	Polychaete	0.0906	0.0315	2.875	10	.02
Chiridota hawaiiensis	Sea cucumber	−0.0145	0.3885	−0.037	10	.97
Hemichordate sp. 2	Hemichordate	0.1529	9.2230	0.685	10	.51
Tellinid sp. 1	Bivalve	−0.5070	0.3996	−1.269	10	.23
Polychaete sp. 4	Polychaete	0.0097	0.2721	0.356	10	.73
Uca tetragonum	Crab	0.0598	1.6043	0.037	10	.97

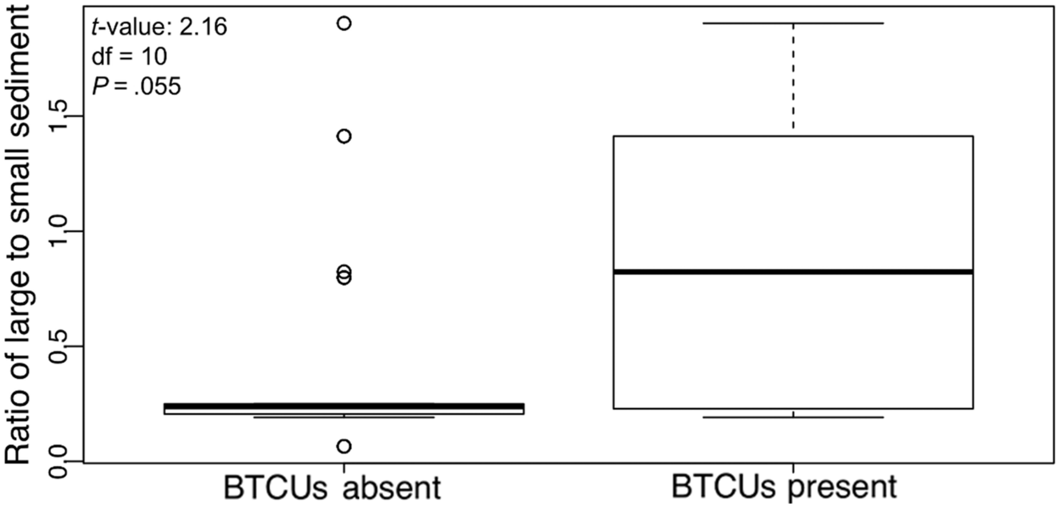

FIGURE 6. Presence of Bristle-thighed Curlews (BTCUs) averaged over all low tides at each site for ratio of large to small sediment grain size.

abundance and sediment grain size ratio (estimate = 0.048 ± 0.057, df = 6, *t*-value = 0.84, *P* = .43).

Focal Sampling

Mean peck rate for all the curlews observed was 4.33 ± 1.11 pecks per minute. There was no significant difference in the presence/absence of pecking behavior between control and high impact categories (estimate = 28.919 ± 254,817, *t*-value = 0.00011, df = 5, *P* = .99), between control and low impact categories (estimate = –0.647 ± 1.30, *t*-value = –0.49892, df = 5, *P* = .64), between high and low impact categories (estimate = –29.566 ± 254,813, *t*-value = –0.00011, df = 5, *P* = .99), or among the different sites (ANOVA, $F_{(7,30)}$ = 0.71, *P* = .66).

Excluding observations without pecking behavior, there was no significant difference in average pecking rate between control and high impact categories (estimate = 1.62 ± 2.54, *t*-value = 0.636, df = 5, *P* = .55), between control and low impact categories (estimate = −1.63 ± 4.01, *t*-value = −0.41, df = 5, $P = .69$), between high and low impact sites (estimate = −3.259 ± 3.785, *t*-value = −0.8609, df = 5, $P = .43$), or among sites (ANOVA, $F_{(7,24)} = 2.28$, $P = .06$). Additionally, average pecking rate was not significantly correlated to *N. tahitiensis* abundance (estimate = −0.002 ± 0.016, *t*-value = −0.116, df = 5, $P = .91$).

DISCUSSION

According to our data, degree of historical land impact did not influence Bristle-thighed Curlew habitat choice. But while curlews did not systematically prefer one impact category over another, they were significantly more likely to be found in 2 of the 13 sites (HI1 and HI5), and both of these preferred flats were in the high impact category. These two sites had higher abundances of *Malacoceros* polychaetes, suggesting that this polychaete may be an important prey item. Curlew presence was also positively correlated, although not significantly so, with coarse sediment. The highest sediment ratios occurred at sites HI1, HI5, LI1, and LI2, but the latter two sites had low abundance of *Malacoceros* polychaetes.

Contrary to our predictions, curlew presence/absence and abundance were not significantly correlated with fiddler crab abundance, suggesting that fiddler crabs may not be a preferred prey item on Palmyra. It is possible that fiddler crab abundance may be high enough that curlews do not need to forage at sites with the highest crab densities to meet their dietary requirements. Alternately, curlews may be foraging for fiddler crabs at night, with patterns of nighttime habitat use differing from the ones we detected during their diurnal foraging. While we incidentally captured some nighttime foraging with the camera traps, we excluded these data from analysis because the bright flash and limited visibility of the trail camera would have biased our measures of curlew abundance. Because it seems that curlews do forage on the flats at night, it would be worthwhile to design sampling to capture these behaviors and compare them to patterns observed during daylight.

Curlew presence was positively related to the presence of *Malacoceros* sp. polychaetes. Although no past studies have documented polychaetes in *N. tahitiensis* diets, the birds are known to prey on a broad range of invertebrates and to be fairly opportunistic in prey choice (Bartsch 1922, Bakus 1967, Ely and Clapp 1973, Gill and Redmond 1992, Marks and Hall 1992). Other species of curlews, such as Long-billed Curlews (*N. americanus*) and Whimbrels (*N. phaeopus*), are known to feed on marine polychaetes in mud and sand flats at nonbreeding sites (Velásquez and Navarro 1993; Perez-Hurtado, Goss-Custard, and Garcia 1997; Leeman et al. 2001). On Palmyra Atoll, Bristle-thighed Curlews were often observed handling both worms and fiddler crabs on sand flats (A. S. Guerra and C. L. Wood, pers. obs.). Therefore, it is possible that curlews prefer sites HI1 and HI5 due to greater prey availability.

Although curlew presence was more likely at sites with high abundance of potential prey items, pecking rate was not higher at these sites. Pecking is a searching and prey-capture attempt behavior in shorebirds, and not all pecks are successful in capturing prey (Turpie and Hockey 1993). Sandpipers have been found to have an increased ratio of successful to unsuccessful pecks in areas of high prey biomass relative to areas of low prey biomass (Goss-Custard 1970). In Whimbrels, prey capture is unrelated to pecking rate and hypothesized to be associated with tactile foraging when foraging in mud (Turpie and Hockey 1997). In our study, we could not distinguish between successful and unsuccessful pecks, and it is therefore possible that physical characteristics of the flat led to similar patterns of tactile foraging, but different foraging success rates.

The positive (although only marginally significant) relationship between ratio of large to small sediment and *N. tahitiensis* presence ($P = .055$) suggests that curlews may choose to forage at sites with coarser sediment. Grain size can alter sediment's resistance to the movement of bird bills, thus influencing bird distributions by affecting their foraging success. Past studies have found that the abundance and distribution of invertebrate prey varies with the physical characteristics of the tidal habitat (Quammen 1982, Velásquez and Navarro 1993, Danufsky and Colwell 2003), though we found no significant correlation between the abundance of *Malacoceros* sp. polychaetes and sediment grain size. However, particle size of substrates may affect foraging behavior of shorebirds; probing shorebirds favor fine sediment, while shorebirds such as curlews peck at the surface prey found on coarser sediment (Colwell 2010). This is consistent with our finding of higher curlew abundance at sites with coarser sediment. Eastern Curlews (*N. madagascariensis*) feeding on intertidal flats in Eastern Australia were found predominantly in coarser sand sediment as it offers less resistance to pecking behavior than finer substrates do (Finn, Catterall, and Drizcoll 2007). Therefore, larger sediment grain size might allow for an increased foraging efficiency at HI1 and HI5.

Our results suggest that a combination of factors, such as prey availability and sediment characteristics, may determine *N. tahitiensis* habitat preferences. Although the degree of land reclamation impact on a site was not significantly related to the presence/absence or abundance of curlews, it is important to consider that the two sites that were preferred by curlews were both highly impacted. Our study highlights the importance of considering shorebird habitat preferences when planning conservation measures. With regard to future restoration initiatives on Palmyra Atoll, our study suggests that lagoon restoration might decrease Bristle-thighed Curlew habitat. In particular, the data reveal the importance of sites HI1 and HI5 for curlews. The lack of significant difference in curlew abundance among sites where curlews were present could indicate a flexibility to move on to another foraging site once one becomes unsuitable. We suggest that care should be taken with restoration near these sites to ensure that they are not substantially altered in any restoration project, as they might provide an important foraging habitat; their alteration could reduce the overall value of the atoll as a foraging ground for curlews. Further research should focus on predicting the potential for change in curlew carrying capacity that could result from restorations of the entire lagoon. More information on habitat use of Bristle-thighed Curlews is necessary to fully assess the potential impacts of restoration on the availability of curlew habitat on Palmyra, particularly studies across the entire winter season and with an effort to identify specific prey types on Palmyra Atoll.

Notably, our results appear to suggest that Bristle-thighed Curlews are relatively adaptable to past intertidal disturbance, as their preferred sites were ones that were highly impacted; this is a positive prognosis for this vulnerable bird. However, more information is needed on the effects of ongoing human disturbance and whether the key factor in their success at Palmyra Atoll is that human disturbance remains only as a legacy effect.

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Literature Cited

Bakus, G. J. 1967. Changes in the avifauna of Fanning Island, Central Pacific, between 1924 and 1963. Condor 69:207–209.

Bartsch, P. 1922. A visit to Midway Island. Auk 39:481–488.

BirdLife International. 2008. *Numenius tahitiensis.* IUCN 2011: IUCN Red List of Threatened Species. Version 2011.2. www.iucnredlist.org.

Brown, S., C. Hickey, B. Harrington, and R. Gill. 2001. United States Shorebird

Conservation Plan. 2nd ed. Manomet Center for Conservation Sciences, Manomet, Massachusetts.

Burger, J., and M. Gochfeld. 1991. Human activity influence and diurnal and nocturnal foraging of Sanderlings (*Calidris alba*). Condor 93:259–265.

Colin, P. L., and C. Arneson. 1997. Tropical Pacific invertebrates: A field guide to the marine invertebrates occurring on tropical Pacific coral reefs, seagrass beds, and mangroves. Coral Reef Research Foundation, Beverly Hills, California.

Collen, J. D., D. W. Garton, and J. P. A. Gardner. 2009. Shoreline changes and sediment redistribution at Palmyra Atoll (Equatorial Pacific Ocean): 1874–present. J. Coast. Res. 253:711–722.

Colwell, M. A. 2010. Shorebird ecology, conservation and management. University of California Press, Berkeley.

Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: A review. Wildl. Soc. B. 27:571–581.

Danufsky, T., and M. A. Colwell. 2003. Winter shorebird communities and tidal flat characteristics at Humboldt Bay, California. Condor 105:117–129.

Dawson, E. Y. 1959. Changes in Palmyra Atoll and its vegetation through the activities of man, 1913–1958. Pac. Nat. 1:1–51.

Ely, C. A., and R. B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Research Bulletin 171. Smithsonian Institution, Washington, D.C.

Engilis, A., Jr., and M. Naughton. 2004. U.S. Pacific Islands Regional Shorebird Conservation Plan: U.S. Fish and Wildlife Service, Portland, Oregon.

F.A.B. Pearl Harbor, photographer. 1935*a*. Palmyra Island. Photograph collection. United States Navy. National Archives, San Francisco, California.

———. 1935*b*. Palmyra Island. West Lagoon. Looking North [No. PH18096]. Photograph. United States Navy, 1 November. National Archives, San Francisco, California.

———. 1935*c*. Palmyra Island. East Lagoon. Looking South [No. PH18915]. Photograph. United States Navy, 1 November. National Archives, San Francisco, California.

Finn, P. G., C. P. Catterall, and P. V. Drizcoll. 2007. Determinants of preferred intertidal feeding habitat for Eastern Curlew: A study at two spatial scales. Aust. Ecol. 32:131–144.

Gelman, A. 2007. The ¼- power transformation [blog]. Statistical Modeling, Casual Inference, and Social Science. 2 January. http://andrewgelman.com/2007/01/02/the_14power_tra/.

Gill, R. E., R. B. Lanctot, J. D. Mason, and C. M. Handel. 1990. Observations on habitat use, breeding chronology and parental care in Bristle-thighed Curlews on the Seward Peninsula, Alaska. Wader Study Group Bull. 61:28–36.

Gill, R. E., and R. L. Redmond. 1992. Distribution, numbers, and habitat of Bristle-thighed Curlews (*Numenius tahitiensis*) on Rangiroa Atoll. Notornis 39:17–26.

Gosliner, T. M., D. W. Behrens, and G. C. Williams. 1996. Coral reef animals of the Indo-Pacific. Sea Challengers, Monterey, California.

Goss-Custard, J. 1970. The responses of redshank to spatial variations in the density of their prey. J. Anim. Ecol. 39:91–113.

Hoover, J. P. 2006. Hawai‘i’s sea creatures: A guide to Hawai‘i’s marine invertebrates. Mutual Publishing, Honolulu, Hawai‘i.

Junk, W. J. 2002. Long-term environmental trends and the future of tropical wetlands. Environ. Conserv. 29:414–435.

Kessel, B. 1989. Birds of the Seward Peninsula, Alaska: Their biogeography, seasonality and natural history. University of Alaska Press, Fairbanks, Alaska.

Kirchner, J. 1995. Data analysis toolkit #3: Tools for transforming data [notes]. Earth and planetary science: EPS 120—analysis of environmental data. University of California, Berkeley. http://seismo.berkeley.edu/~kirchner/eps_120/EPSToolkits.htm.

Lanctot, R. B., R. E. Gill, T. L. Tibbitts, and C. M. Handel. 1992. Brood amalgamation in the Bristle-thighed Curlews *Numenius tahitiensis:* Process and function. Ibis 137:559–569.

Leeman, L. W., M. A. Colwell, T. S. Leeman, and R. L. Mathis. 2001. Diets, energy intake, and kleptoparasitism of nonbreeding Long-billed Curlews in a Northern California estuary. Wilson Bull. 113:194–201.

Madrigal, L. G. 1999. Field guide of shallow water marine invertebrates of American Samoa. American Samoa Government Department of Education, Pago Pago, American Samoa.

Magier, S., and L. Morgan. 2012. A brief history of human activities in the US Pacific Remote Islands. Marine Conservation Institute, Seattle, Washington.

Maragos, J., A. M. Friedlander, S. Godwin, C. Musburger, R. Tsuda, E. Flint, O. Pantos, P. Ayotte, E. Sala, S. Sandin, S. McTee, D. Siciliano, and D. Obura. 2008. US coral reefs in the Line and Phoenix Islands, Central Pacific Ocean: Status, threats and significance. Pages 643–654 *in* B. M. Riegl and R. E. Dodge, eds. Coral reefs of the USA. Springer, New York.

Maragos, J., J. Miller, J. Gove, E. DeMartini, A. M. Friedlander, S. Godwin, C. Musburger, M. Timmers, R. Tsuda, P. Vroom, E. Flint, E. Lundblad, J. Weiss, D. Siciliano, R. Brainard, D. Obura, S. Ferguson, and B. Mundy. 2008. US coral reefs in the Line and Phoenix Islands, Central Pacific Ocean: History, geology, oceanography, and biology. Pages 595–641 *in* B. M. Riegl and R. E. Dodge, eds. Coral reefs of the USA. Springer, New York.

Marks, J. S. 1993. Molt of Bristle-thighed Curlews in the Northwestern Hawaiian Islands. Auk 110:573–587.

Marks, J. S., and C. S. Hall. 1992. Tool use by Bristle-thighed Curlews feeding on albatross eggs. Condor 94:1032–1034.

Marks, J. S., and R. L. Redmond. 1994. Conservation problems and research needs for Bristle-thighed Curlew *Numenius tahitiensis* on their wintering grounds. Bird Conserv. Int. 4:329–341.

Marks, J. S., L. T. Tibbitts, R. E. Gill, and B. J. McCaffery. 2002. Bristle-thighed Curlew (*Numenius tahitiensis*). *In* A. Poole, ed. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York. http://bna.birds.cornell.edu/bna. doi:10.2173/bna.705.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. U.S. Department of the Interior, National Biological Service, Washington, D.C.

O'Brien, T. G., and M. F. Kinnaird. 2008. A picture is worth a thousand words: The application of camera trapping to the study of birds. Bird Conserv. Int. 18:S144–S162.

Perez-Hurtado, A., J. D. Goss-Custard, and F. Garcia. 1997. The diet of wintering waders in Cádiz Bay, southwest Spain. Bird Study 4:45–52.

Quammen, M. L. 1982. Influence of subtle substrate differences on feeding by shorebirds on intertidal mudflats. Mar. Biol. 71:339–343.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Severns, M. 2001. Hawaiian seashells. Island Heritage, Waipahu, Hawai'i.

Silveira, L., A. T. A. Jácomo, and J. A. F. Diniz-Filho. 2003 Camera trap, line transect census and track surveys: A comparative evaluation. Biol. Conserv. 114:351–355.

Stoddart, D. R. 1968. Catastrophic human interference with coral atoll ecosystems. Geography 53:24–40.

Turpie, J. K., and P. A. Hockey. 1993. Comparative diurnal and nocturnal foraging behavior and energy intake of premigratory Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeopus* in South Africa. Ibis 135:156–165.

———. 1997. Adaptive variation in the foraging behavior of Grey Plover *Pluvialis squatarola* and Whimbrel *Numenius phaeopus.* Ibis 139:289–298.

U.S. Fish and Wildlife Service, Pacific Region. 2011. Final environmental impact statement: Palmyra Atoll National Wildlife Refuge rat eradication project. U.S. Fish and Wildlife Service, Pacific Region, Portland, Oregon.

Velásquez, C. R., and R. A. Navarro. 1993. The influence of water depth and sediment type on the foraging behavior of whimbrels. J. Field Ornithol. 64:149–157.

Warnock, N., C. Elphick, and M. A. Rubega. 2001. Shorebirds in the marine environment. Pages 582–606 *in* E. A. Schreiber and J. Burger, eds. Biology of marine birds. CRC Press, Washington, D.C.

Wodzicki, K. 1981. Some nature conservation problems in the South Pacific. Biol. Conserv. 21:5–18.

Yates, M. G., J. D. Goss-Custard, C. McGrorty, K. H. Lakhani, V. Le, S. E. A. Dit Durell, R. T. Clarke, W. E. Rispin, I. Moy, T. Yates, R. A. Plant, and A. J. Frost. 1993. Sediment characteristics, invertebrate densities and shore-bird densities on the inner banks of the Wash. J. Appl. Ecol. 30:599–614.