POPULATION SIZE AND HABITAT OCCUPANCY OF THE ENDANGERED MARIANA CROW

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Abstract. I present data on the Mariana Crow for an extensive but previously unavailable set of population and habitat surveys from 1992-1993. From these, I 1) compute a series of population estimates from that period during which Mariana Crow numbers were first entering a precipitous decline, 2) quantitatively assess the habitats occupied by individual birds and thereby provide a view of the range of habitats occupied during a time when the species was still widespread, and 3) provide the first direct wet-dry season comparisons of populations and habitat occupancy. Surveys yielded significantly different wet (943) and dry season (459) population estimates, which suggested wet season courtship activity preceding dry season nesting when birds became more secretive. Moreover, they indicated that the critical turning point in population decline was after 1995. Forest was the principal habitat type occupied during both wet and dry seasons, with savanna present less than half as often as forest, although birds occupied a range of additional habitats. The species was more versatile in habitat use than is often assumed, as rates of habitat occupancy and availability were similar. Versatility is an advantage for populations confined to small islands that periodically suffer catastrophic habitat damage due to typhoons.

The Mariana Crow (*Corvus kubaryi*) is endemic to the Mariana Islands of the western tropical Pacific, where it is historically known from the islands of Guam and neighboring Rota although, based on multiple prehistoric extinctions that have occurred in the island chain's avifauna (Steadman 1992, 1999), it may once have had a wider distribution. Due to the precarious nature of the species' population on Guam, it was given U.S. Endangered status in 1984 (USFWS 1984). By the 1980s, Jenkins (1983) believed that the Rota population had also declined, perhaps by 50% (National Research Council 1997), although quantitative population estimates were only first made there in 1982 (Engbring et al. 1986). Since the 1990s, it has been extinct on Guam due to predation by the brown tree snake (*Boiga irregularis*; Wiles et al. 2003). However, into the 1990s it remained widespread on Rota (National Research Council 1997). Since that time, multiple quantitative population surveys (e.g., Fancy et al. 1999, Amar et

al. 2008, Camp et al. 2015) have documented a substantial decline, with numbers most recently estimated at 178 (Kroner and Ha 2018). Phenomena driving the population decline include particularly a reduction of first year survival of young (Ha et al. 2010), which appears to be the consequence of such factors as predation by feral cats and disease (Zarones et al. 2015, Faegre 2017).

Habitat degradation also has been suggested as a contributing factor to the decline (National Research Council 1997), although only limited evidence exists as to what qualifies as suitable habitat. Preferred habitat historically has been described as being native forest (Baker 1951, Engbring et al. 1986). More recent study has demonstrated that in the present small population, nests are typically placed in mature native forest (Ha et al. 2011). However, Faegre (2017) found no prey or vegetation factors that were predictive of either core use areas near nests or outer areas of home ranges. Similarly, when the species was more common, Tomback (1986) reported Mariana Crows to be omnivorous and to use not only mature forest but also stunted strand forest and to use both native and introduced trees. Moreo-

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FIG. 1. Mature limestone forest on a steep slope transect leading to the Sabana.

ver, in the 1990s Morton et al. (1999) reported nesting birds in only partially forested habitats, although the nests themselves were placed in interior forest, with an average distance from forest edge being only 62 m.

In studies on other Mariana Island bird species, I found many to be versatile in terms of foraging ecology and microhabitat use (Craig 1990, Craig and Beal 2002), although population densities indeed tended to be greatest in native forest (Craig 2021a). My 1990-1993 observations on the Mariana Crow similarly suggested that the species might be like many of the world's crows in being more of an ecological generalist than is typically assumed, as I observed birds using low forest strand, mixed native-alien second growth forest, alien thickets and even savanna habitats in addition to mature native forest.

Present habitat use can be deceptive in assessing a species' true ecological amplitude. For example, in the case of another critically endangered Rota endemic, the Rota White-eye (*Zosterops rotensis*), the species is presently restricted in its occurrence to cloud forest-like habitats at the highest elevations of the island. Such locations are now designated critical habitat for the species. However, into at least the 1950s the species appeared to have been more widespread at low elevations and even in settled areas (USFWS 2007). Furthermore, observations of the species' foraging and social behavior demonstrated that it was very similar to the supremely versatile Bridled White-eye (*Zosterops conspicillatus*) of neighboring Saipan (Craig and Taisacan 1994). Hence, the present habitat occu-

pancy of this species appears to represent only a fraction of the habitats that it is capable of using.

In this study, I present data from an extensive but previously unavailable set of population and habitat surveys from 1992-1993. From these, I 1) compute a series of population estimates made 10 years after the first estimates and from that period during which Mariana Crow numbers were first entering a precipitous decline, 2) quantitatively assess the habitats occupied by individual birds at the moment of their encounter, thereby providing a view of the range of habitats occupied during a time when the species was still widespread, and 3) provide the first direct wet-dry season comparisons of populations and habitat occupancy.

METHODS

Study areas. Rota (14°09'N, 145°12'E) is a sparsely populated (1,893 residents, U.S. Census Bureau 2020), 85.13 km² raised coral island of volcanic origin that also has a significant exposure of volcanic soil on its south-central flank. It possesses limestone terraces, with the highest a southwestern plateau known as the Sabana that rises to 491 m. Steep slopes descend from most of the Sabana, although the northeastern slope descends gradually to the eastern island lowlands (ca.150 m elevation). The climate is characterized by high humidity, uniform temperatures and typically a December−early June dry season and a late June−November wet season. The dry season has reduced rainfall, easterly trade winds and reduced flowering and fruiting by most native trees, whereas the wet season is largely

windless, has greater rainfall (Young 1989) and has greater flowering and fruiting by native trees (Craig 1996). Typhoons are regular and exert a strong influence on the structure of natural habitats (Fosberg 1960).

Recent estimates indicate that 67.2% of Rota remains forested, with 78.7% of this being native forest. Habitat cover has not appreciably altered since 1976 (Donnegan et al. 2011). The most widespread forest type by far is termed native limestone forest due to its occupying particularly the island's steep limestone slopes (Fig. 1). This forest appears more mesic in character than on the more northerly islands of Saipan, Tinian and Aguiguan, especially on the Sabana plateau (Fig. 2), which is frequently covered by clouds and vegetated by several tree species not found at lower elevations (pers. obs). In level areas planted to sugarcane (*Saccharum officinarum*) prior to World War II (Engbring et al. 1986), second growth comprised of mixed introduced and native trees constitutes 13.0% of forest cover (Fig. 3), with many natives aggressive competitors with alien species (Craig 1994). Areas of planted crop-producing trees like coconuts (*Cocos nucifera*), termed agroforest, account for 5.8% of forest area, and 1.8% is low coastal strand forest that occurs principally along the north-central coast (Fig. 4). The remaining 32.8% of Rota includes 6.6% residential/commercial landscapes, 1.7% cropland, particularly on the Sabana, and 22.8% open ranch land with scattered individual trees and tree copses that I here term savanna habitat (Fig. 5) although small amounts of native swordgrass (*Miscanthus floridulus*) savanna also exist on exposed volcanic soils. Nominal cover by beach and coastal rocks also occurs.

Bird surveys. In 1991, I was tasked by the Division of Fish and Wildlife, Commonwealth of the Northern Mariana Islands, with developing a roadside sampling method for determining the distribution and population size of Mariana Crows, as I had previously developed such surveys for the neighboring island of Saipan (Craig 1996). The study was authorized to assist with assessing environmental impacts of a planned golf resort development. Roadside surveys have the advantage of covering extensive areas quickly during the peak of bird activity and have been used for decades to track population trends of North American birds (Sauer et al. 2017). As the 1982 survey had used the variable circular plot protocol (Reynolds et al. 1980), I continued with this approach. The variable circular plot (VCP) has wide utility in evaluating populations over a variety of terrains, has a well-developed theoretical underpinning that accounts for differential detectability of species (Buckland et al. 2001, Thomas et al. 2010, Research Unit for

FIG. 2. Mature Sabana forest showing dense epiphytic plant growth.

FIG. 3. Secondary lowland forest exhibiting a canopy of non-native flame trees (*Delonix regia*). Note also clouds on the Sabana.

Population Assessment 2020) and has become a standard technique for conducting large-scale surveys of tropical Pacific forest birds (e.g., Scott et al. 1986, Camp et el. 2015, Linck et al. 2020).

Based on four August 1991 calibration surveys, I reduced the time spent at sampling stations from 8 to 5 minutes to minimize the potential for over-counting due to movements by these wide-ranging crows. I also lengthened the distance between sample points from 150 to 402 m (generally 0.25 mi, although the exact distance between points sometimes depended on the peculiarities of the survey route) to maximize the independence of samples, as Mariana Crows are loudly vocal and I often detected them to over 100 m, although only infrequently to 200 m (see also Engbring et al. 1986). The previous 1982 computations may have overestimated populations by counting the same bird from two sampling stations (Plentovich et al. 2005). Using roadside surveys also shortened the survey duration from ca. 4 to 2 hr so that counts could be completed during periods of peak crow activity, which through calibration surveys and other field observations I determined to be the first and last 2 hr of the day, both of which I used equally during this study.

I established eight survey transects (Fig. 6) that counted solely crows and covered most of the island other than settled areas. Transects followed un-paved coral roads, although in many instances the roads were little more than two track paths. De-pending upon road extent, transects had 18-21 survey points, covering a total of 160 points, although in several instances I deleted a point from an individual survey due to local conditions (e.g., temporary inaccessibility of a point). I visited transects in random order in January, April and October, 1992 and January, April and July 1993. Before the era of widely available GPS technology, I plotted the location of points on a USGS topographic map, noting especially the location of aerially visible landmarks with respect to the points to help locate them on the map exactly.

At each point, I estimated the horizontal distance at first detection to each bird encountered. To verify distance estimates, I periodically measured via pacing the distance from a sampling point to the location of a vocalizing bird. I also noted on a USGS topographic map the location of distant birds so that I could directly measure the distance from the map. Furthermore, I relied on my long experience in making distance estimates with this and earlier versions of distance sampling, which dates to 1972 (e.g., Wolgast et al. 1972, Craig 1987).

I conducted surveys under conditions of minimal rain and wind, although particularly during the wet season passing showers sometimes occurred and during the dry season steady wind was routine, although I did not judge it to be strong enough to influence vocalizations of this or other species, particularly in light of my concurrent bird surveys from

FIG. 4. Strand forest on a transect on the northeast coast.

neighboring Saipan, which showed little seasonal shift in bird activity (Craig 1996, 2021a). In one instance, I had a survey briefly interrupted by a total solar eclipse, during which time all bird activity ceased.

Habitat evaluation. In addition to estimating the distance to each bird encountered, I also recorded the compass direction of individuals from sample points for all surveys except April, 1992. Using QGIS 3.16 geographical information systems software, I employed an azimuth/distance plotting tool with data corrected for magnetic north to locate each bird with respect to georeferenced 1994 color aerial photographs of Rota. I then plotted around each location a 20-sided polygon that approximated a 100 m diameter circle with an actual diameter of 108.4 m (0.92 ha). I chose this size circle because it represented only a tiny portion of a bird's home range, which typically extends over hundreds of ha (Faegre et al. 2018), thereby maximizing the probability that measures fell within a home range even given any error in the exact plotting of sightings. Due to golf course development by the time the 1994 photos were taken, I was unable to analyze several polygons that fell within areas cleared for development.

Within each polygon, I digitally measured the habitats present. I initially experimented making measurements with a pixel classification tool but found that I could make more accurate and precise measures, particularly in light of my field notes on

habitats present at each point, by delineating habitats through visual inspection of photographs. I divided habitats into 1) uncultivated forest, 2) savanna, 3) beach, 4) cultivated land, including cropland and agroforest, and 5) residential areas and roads that broke the forest canopy. As noted, forest may be further divided into several categories, but considering the resolution available in 1994 photos and that crows are known to use all forest habitats (Engbring et al. 1986), I chose not to further subdivide the forest category. With measuring tools, I computed the number of square meters of habitat present in each category for each bird detection considered. For statistical analyses, I collapsed savanna and categories other than forest into a single category to eliminate zeros.

Because the Mariana Crow often occurs in family groups and tends to occupy the same area for at least months (Faegre et al. 2018), multiple birds may occur at a sample point and the same individuals may occur from one sampling to the next. Hence, I chose to analyze for habitat occupancy at only one observation/sample point per season in order to ensure the independence of within-season observations. I also eliminated from consideration my several detections of birds estimated to be >200 m distant, as I viewed these to be less accurate assessments of habitat occupancy.

In addition to measuring the habitats occupied by individual birds, I also characterized the habitats along each transect so that I could assess habitats

FIG. 5. Savanna habitat along a transect exhibiting grassland and interspersed tree copses.

occupied vs. habitats present in the sampled area. Doing so also permitted assessment of how well the survey transects sampled habitats present on the island. To characterize, I constructed a 200 m wide buffer around each transect (400 m total width), with this distance chosen to correspond with the maximum distance at which I evaluated individual birds' habitat use. Within the sampling zone, I digitally delineated the boundaries of the same five habitat categories examined for individual birds. I computed the area covered by each category using QGIS measurement tools. In those few instances where transects had overlapping sampling zones, I evaluated habitats in that zone for only one of the transects. I deleted from consideration areas obscured by cloud cover.

Analysis. I computed population densities with Distance 7.3 software (Thomas et al. 2010, Research Unit for Population Assessment 2020), consulting also the protocols of Buckland et al. (2001) in developing detection functions. As the species often occurred in social groups, I performed analyses with clusters as the basis of density measurement. Based on exploratory plots of species detection probability vs. detection distances, I grouped similar observations into six categories, with interval cut points placed between favored rounding distances to minimize data "heaping" and to improve robustness of density estimation. I explored the fit of detection data to six models recommended by Buckland et al. (2001): uniform/cosine, uniform/ simple polynomial, half normal/cosine, half normal/ hermite polynomial, hazard rate/cosine and hazard rate/simple polynomial. As also recommended by Buckland et al. (2001), I truncated detection data for individual species to eliminate the largest 5% of values, which facilitated model fitting by eliminating outliers. I used the multiple covariate distance sampling engine, entering year as a covariate, to yield a global model that produced a smooth curve with near 100% detection probability at the left shoulder, evaluated fit by visual inspection of plotted data, with Akaike's Information Criterion and with chi-square goodness of fit tests and empirical computation of variance. I post-stratified analyses to yield density estimates for each transect visit and used these in testing for wet-dry season differences of occurrence.

Because I gathered population data at the same sites over a series of years, they were repeated measures. Hence, I employed repeated measures analysis of variance in examining results. I entered season as a within-subject effect and visits to transects as a between-subject effect. Individual transect measures were observations within years. I checked the fit of data to model assumptions with data plots, frequency histograms, normal Q-Q plots, residual plots, Levene's homogeneity of variance tests, Shapiro-Wilk normality tests and Box's M test.

In the case of habitat data, a conservative interpretation is that between-season comparisons of

FIG. 6. Distribution of eight survey transects on Rota, Mariana Islands, showing the location of survey points.

habitats are also repeated measures on the same birds, although the reality is that many birds upon which I made measures months apart were likely separate individuals. Parametric assumptions were poorly met by the data, so to compare wet vs. dry season cover by forest and savanna/human habitats I employed both a Wilcoxon Signed Rank related samples nonparametric test as a conservative approach and a Mann−Whitney U independent samples test as a more liberal approach. As forest and savanna tests are mirror images due to their being parts of the same whole, they produced the same result so I report only forest results here.

RESULTS

Populations. I detected 341 individuals during this study, which produced a sample size of 201 for cluster-based distance analysis. Analysis yielded a detection function based on a half-normal/cosine model ($x^2 = 0.32$, df = 3.00, $P = 0.96$; Fig. 7). Post-stratification of results by season yielded a wet season population estimate of 943 (95% CI = 697−1272) and a dry season estimate of 459 (95% CI = 341−619). Repeated measures analysis of variance on seasonal population estimates (Table 1) indicated that they differed significantly (within-season $F = 8.47$, df, = 1,14, $P = 0.01$). However, I found no significant differences among visits (between-season $F = 0.37$, df, = 1,14, $P = 0.55$) or a significant season x visit interaction (within-season $F = 0.87$, df, = 1,14, $P = 0.37$).

Habitats. I made 63 measures of habitat occu-pancy by individuals during the wet season and an additional 45 measures during the dry season. Forest was by far the principal habitat type occupied during both seasons, with savanna present less than half as often as forest (Table 2), although individual birds occurred in solely savanna habitat. Wet season savanna occupancy showed a small increase and forest occupancy a similar small decrease compared with the dry season. Wilcoxon tests on forest cover found these seasonal differences to be non-significant ($Z = −0.56$, $P > 0.58$), as did Mann−Whitney tests ($U = −0.38$, $P > 0.70$). Other habitat types were used in only nominal amounts during both seasons, although I observed birds occupying areas that included beaches, cropland and a variety of forest types: coastal strand forest, low thicket-like forests, agroforest and mixed native/introduced forest.

Habitat occupancy measures showed that forest use was greater than and savanna use less than its availability along transects, particularly during the dry season, although neither season yielded results significantly different from availability (dry: Yates $x^2 = 2.28$, df = 1, $P = 0.12$; wet: Yates $x^2 = 0.55$, df = 1, $P = 0.46$, with savanna, human cover and the <2% combined cover by cropland and beach pooled for analysis to yield cell values >5). Habitat availability as measured along transects from 1994 photos (covering 23.02 km², or 27.04% of total island area) showed forest cover to be less than and savanna cover to be more than that of Donnegan et al.'s (2011) recent estimates, although again not signifi-

TABLE 1. Seasonal population density estimates (birds/km^2) for each transect.

Transect		Season				
	Dry				Wet	
	Jan. 1992	Apr. 1992	Jan. 1993	Apr.1993	Jul. 1993	Oct. 1993
1	3.5	12.1	5.4	3.8	11.5	8.6
2	3.5	5.2	8.6	3.3	17.3	28.0
3	10.4	15.5	5.2	1.7	6.9	17.3
4	10.5	6.9	8.2	1.6	11.5	19.7
5	6.9	3.5	6.9	1.7	6.9	1.7
6	6.9	3.8	0.0	17.3	17.3	16.3
7	0.0	1.7	0.0	1.6	1.7	4.9
8	1.7	5.2	1.6	8.2	5.2	6.6
mean	5.4	6.7	4.5	4.9	9.8	12.9
SD	4.1	4.5	3.8	5.9	6.0	9.4

cantly so (Yates $\chi^2 = 0.35$, df = 1, $P = 0.55$; Table 2).

DISCUSSION

Comparison of wet and dry season population estimates provides strong evidence that the apparent size of the Mariana Crow population is influenced by the season of survey. The species breeds year-round (Engbring et al. 1986, Morton et al. 1999), with peak breeding described variously: curtailed from May to July (Engbring et al. 1986), Oct.-March (Lusk and Taisacan 1996), Aug.-Dec. (National Research Council 1997), Aug.-Feb. (USFWS 2005) and Aug.-April (Zarones et al. 2015). Hence, breeding appears frequent in at least portions of both the wet and dry season. However, my population estimates were consistently highest in both of my wet season measures and particularly October, which suggests that increased vocalization and, thus, detectability occurred during these times. This observation may be related to findings for several other Marianas bird species that showed evidence of molt in the late wet season and peak breeding in the dry season, which thereby segregates these energetically expensive activities (Craig 2021b). A peak in wet season vocalization could indicate courtship or family group activity preceding dry season nesting when birds become more secretive.

Compared with Engbing et al.'s (1986) estimate of 1491 individuals based on 254 station visits in April 1982 (as revised by Camp et al. 2015), my population estimates were consistently far lower.

My two April surveys of 321 station visits yielded an average of 496 crows. However, Jenkins and Aguon (1981) found birds at 16% of 19 survey stations in April, whereas I found them during 21.5% of 1048 station visits overall and 17% of 321 April visits. Moreover, 1988 roadside counts reported by Camp et al. (2015, supplemental table S6) had occurrences of 26.0% at 96 December stations and 20.8% at 90 August stations compared with 15.2% at 322 January stations and 27.5% at 160 July stations in this study. These observations provide evidence of count-to-count variation but also some evidence that Engbring et al. (1986) may have over-estimated the population due to overcounting and that numbers may not have changed dramatically from 1982 to 1992−1993.

Other population estimates since 1992−1993, standardized by Camp et al. (2015), include 891 (95% CI = 500−1935) from an October−November 1995 survey of 311 stations (Fancy et al.1999) using Engbring et al.'s (1986) procedure. My Oct. 1992 estimate was 1058 (95% CI = 788−1421), or close to Camp et al.'s (2015) computation. Camp et al. (2015) further reported a 1998 estimate of 407 (95% CI = 212−899) for VCP data. In contrast, Plentovich et al. (2005) counted 117 breeding pairs in 1998, whereas Zarones et al. (2015), based on counts of paired and unpaired birds, found 144 individuals in 2007−2008. Camp et al. (2015) also reported a 2003 VCP estimate of 244 (95% CI = 115−620) and a 2012 VCP estimate of 81 (95% CI = 30−202), with birds appearing at 4% of 666 station visits for this latter estimate. The most recent estimate is 178 for 2013−2014 (Kroner and Ha 2018).

TABLE 2. Wet/dry season principal habitat associations (ha) of Mariana

Crows, with % island habitat availability from Donnegan et al. (2011).

		Habitat		
	N	Forest	Human	Savanna/other
Dry	45			
mean		0.67	0.03	0.22
SD		0.29	0.04	0.29
% cover		73	3	24
Wet	63			
mean		0.63	0.03	0.28
SD		0.33	0.03	0.33
% cover		68	3	29
% transect habitat availability		62	5	33
% island habitat availability		67	7	26

Hence, despite some variation in results among studies, as also concluded by Camp et al. (2015), populations appear to have declined steadily to the present, with my data suggesting that the critical turning point was after 1995.

Previous observers have noted that few crows inhabited the Sabana plateau (Engbring et al. 1986, Camp et al. 2015) and indeed in this study I recorded no birds on my 48 visits to the eight transect points present at the summit of the Sabana, although detections of birds on the slopes leading to the Sabana were frequent. Similarly to Engbring et al. (1986), my transect east of Songsong Village, which is at the western end of Rota, had the least sightings of any transect, although a second transect just southeast of Songsong in the approximate location of Engbring et al.'s (1986) Songsong transect produced multiple observations to the edge of residential development.

Habitat data provided evidence that the Mariana Crow is indeed associated principally with forest habitat. However, it also demonstrated that it is more versatile in the range of habitats it occupies than is often assumed in that habitat occupancy and availability did not differ greatly, particularly during the wet season. As I have noted for other Marianas bird species (Craig and Beal 2002), versatility is an advantage for populations confined to small islands that periodically suffer catastrophic habitat damage due to typhoons. Supporting albeit weaker evidence for this view comes from Amar et al. (2008), who reported no difference in number of individuals encountered between forest and open habitats. Moreover, Camp et al. (2015) found no association of bird occurrence to vegetation but a weak association with elevation, with birds largely absent from higher elevation. In both these instances, the studies were not specifically designed to assess habitat use.

ACKNOWLEDGEMENTS

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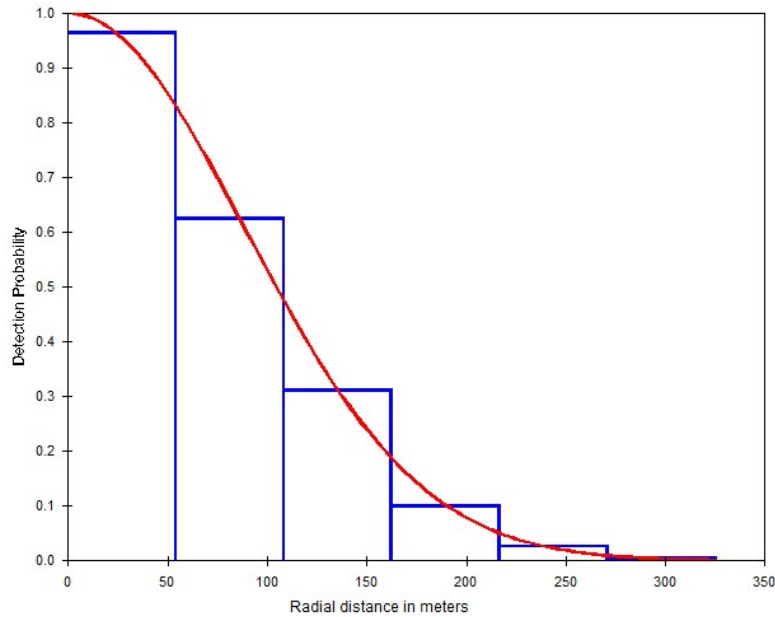BUCKLAND, S.T., D.R. ANDERSON, K.P. BURNHAM, J.L. LAAKE, D.L. BORCHERS and L. THOMAS.

FIG. 7. Half-normal/cosine detection function for the Mariana Crow, demonstrating near 100% detection probability near the left curve shoulder.

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