Behavioral Ecology of the Mariana Crow (*Corvus kubaryi*): Age-related Foraging, Spatial Behavior, Habitat Selection, and Correlates of First Year Survival

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Abstract

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There is little information on Mariana Crow foraging, spatial behavior, habitat selection, or the correlates of first year survival, yet these topics of study are critical for management and species recovery. In this work, we demonstrate that adult crows forage more frequently on hermit crabs, which they process using complex behaviors, while fledglings rely more on fruits, and insect larvae, which they procure and process with simple behaviors. Adults acquire more food items from the ground than other ages due to their frequent predation of hermit crabs. We also demonstrate that fledglings have reduced mobility during the first 4-10 weeks post-fledging and that, after controlling for this low post-fledging mobility, sub-adult Mariana Crows range over larger areas than fledglings and family groups. Regardless of age, Mariana Crows have dynamic, shifting home ranges which lack stable boundaries. Mariana crow family groups have core areas that they return to regularly, even as ranges shift. However, we found no evidence of habitat differences in core areas, compared to infrequently used, outer portions of ranges. In our radio-telemetry study of 22 fledglings, only 45% of individuals survived their first year and the majority of deaths were ruled feral cat predations, based on the appearance of the remains. Fledglings with shorter wings had reduced home ranges and daily movements, and lower first year survival. These results highlight vulnerabilities resulting from foraging, spatial behavior, and physical development at fledging. We emphasize the importance of learning in the development of foraging behaviors, the need for habitat-wide predator management to improve first year survival, and need for continued research into the mechanisms leading to poorly developed fledglings with reduced first year survival.

Table of Contents

Chapter 1: Age-related diet and foraging behavior of the critically endangered Mariana Crow (*Corvus kubaryi*)

Chapter 2: Spatial Ecology of the Mariana Crow: A Radio-tracking Study

Chapter 3: Habitat Selection of the Mariana Crow

List of Figures

List of Tables

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Chapter 1: Age-related differences in diet and foraging behavior of the critically endangered Mariana Crow (*Corvus kubaryi*)

Introduction

Age-related differences in diet and foraging behavior have been attributed to many factors, including the different nutritional needs or optimal foraging strategies of each age class (Engen & Stenseth 1989), different food resources in habitats occupied by adult versus immature animals (Penteriani *et al.* 2011), and changes in foraging ability due to physical maturation and learning (MacLean 1986, Enoksson 1988, Yoerg 1998). Immature animals are usually inefficient foragers (Sullivan 1988, Yoerg 1994, Heise & Moore 2003, Natasha Vanderhoff & Eason 2008) and rely on foods that are easiest to procure (Yoerg 1994). Most bird species exhibit age-dependent survival in which younger individuals have higher mortality rates and increased susceptibility to starvation and predation (Lack 1954, Sullivan 1988, Martin 1995).

Studies comparing the foraging behaviors of juvenile and adult birds widely report that juveniles are less adept in one or more components of foraging (Marchetti & Price 1989, Wunderle 1991). Both motor maturation and learning are important for the development of foraging behaviors in birds (Tebbich *et al*. 2001, Slagsvold and Wiebe 2011, Brumm and Teschke 2012), and some species do not become proficient in the full spectrum of species-typical foraging behaviors for months or years after reaching nutritional independence (Heinsohn *et al*. 1988, Heinsohn 1991, Bluff *et al*. 2010, Holzhaider *et al*. 2010a,b).

Island ecosystems are highly susceptible to the effects of invasive species and habitat transformation (Brook *et al*. 2008, Szabo *et al*. 2012), both of which can lead to changes in food resources (Banko *et al.* 2013, George *et al.* 2013). Knowledge of the age-related diets and foraging behaviors of island-endemic species may help wildlife managers predict species' responses to changes in availability of food resources, and may highlight age- or season-specific needs or vulnerabilities. Information on diet and foraging behavior may also be used to improve assessments of habitat quality and to improve diets and enrichment opportunities for captive animals.

The Mariana Crow (*Corvus kubaryi*) is a critically endangered island-endemic corvid whose single remaining population is on the island of Rota, Commonwealth of the Northern Mariana Islands (CNMI), and is declining. The decline has been attributed to habitat loss and degradation, persecution by humans, predation and competition from introduced species, and inbreeding depression (Morton *et al*. 1999, Plentovich *et al*. 2005, USFWS 2005, Wiewel *et al*. 2009, Sussman *et al*. 2015). Little evidence is available to support these ideas, although recent evidence from radio-telemetry studies suggests that predation from feral cats (*Felis catus*) may be an important cause of mortality for fledgling, sub-adult, and adult Mariana Crows (S. Faegre and R. Ha, unpublished data).

The Mariana Crow is an opportunistic omnivore that forages within primary and secondary limestone forest, using all forest strata, from the ground to the supercanopy (Tomback 1986). Previous studies have identified common food items as insects, including *Ensifera* (grasshoppers and crickets), *Mantodea* (mantids), *Dermaptera* (earwigs), and *Lepidoptera* larva (moths and butterflies); small vertebrates including *Lacertilia* (lizards), immature *Rattus* (rats), *Aves* (birds) eggs, and nestlings; as well as *Coenobita* hermit crabs, and plant-based items such as fruits, seeds, flowers, and bark (Beaty 1967, Jenkins 1983, Tomback 1986, Michael 1987).

However, quantitative information on diet is lacking and the effects of age and season on diet and foraging behavior are unknown.

In this study, we describe the diets and foraging behaviors of wild crows during three life stages (fledgling, sub-adult, and adult), as well as that of two captive-reared crows during their first 11 months post-release. We hypothesized that age-related differences in diet and foraging behavior of the Mariana Crow would occur due to physical maturation and learning during the fledgling and sub-adult periods. During direct observations of wild Mariana Crows, we counted the frequencies with which fledglings, sub-adults, and adults captured foods in different categories. We predicted that adults would more frequently capture crabs, which are processed using complex sequences of behaviors (S. Faegre, pers. obs.), while fledglings would more frequently obtain fruits, seeds and plant-based items that can be taken and processed using fewer or simpler movements (S. Faegre, pers. obs.). We expected sub-adults to have average levels of food acquisition within all categories due to their intermediate age and presumed foraging abilities. In addition to testing these hypotheses, we explored other statistical relationships between food categories and age classes.

We also compared the frequencies with which the three age classes captured food items from two foraging strata: ground (where items from all food categories can be found), and above ground (where items from all except the “crabs” category can be found). We predicted that, if adults hunt and capture crabs more frequently, this may drive an increase in ground-based food captures for adults, in comparison to other age classes. To assess foraging habitat use at a fine scale, we recorded the forest substrates from which food items were taken. We summarized the frequencies with which foods from each category were taken from each substrate and described foraging techniques that were common to each substrate.

Seasonal weather changes can drive changes in foraging behavior in tropical birds (Jahn *et al.* 2010). Rota experiences a rainy season from July-November and a dry season from January-May, which could result in season-specific needs or vulnerabilities among foraging crows. We hypothesized that Mariana Crows would consume different prey items in the wet vs. dry seasons.

Methods

Study area

Rota is the second most southerly island after Guam in the Mariana Islands, Western Micronesia (14°09'N, 145°12'E). The 85-km^2 island is volcanic in origin with uplifted limestone terraces. The climate is tropical, with high humidity. Wet and dry seasons are typically from July-November and January-May respectively. Rota is located within the Western Pacific typhoon belt and experiences typhoons periodically; however, no typhoons reached Rota during this study.

Radio-tracking and Foraging Observations of Wild Crows

Between March 2010 and March 2013 food items, foraging strata, and foraging substrates were categorized during daily observations of 21 wild, radio-tagged Mariana Crows and at least 15 untagged crows. All crows were aged as fledglings, sub-adults, or adults (defined in Table 1). All untagged crows were members of the same family as the radio-tagged individual(s) with whom they were observed, except for one case in which a neighboring sub-adult was present with a family group.

Of the 21 radio-tagged crows in this study, 16 were tagged as fledglings, one as a sub-adult, and four as adults. Mariana Crows are not cooperative breeders (Morton *et al*. 1999), and nutritional independence from the parents almost always coincides with dispersal from the natal territory (S. Faegre, unpublished data). Crows were classified as fledglings during the period of nutritional dependence on their parents, prior to dispersal, and as sub-adults after reaching independence from their parents but prior to their first nesting attempt. Crows were classified as adults after a nesting attempt, or evidence of it (i.e. crows found caring for fledglings), was observed. The precise number of adults in this study is unknown. However, based on the number of family groups in which unbanded and/or banded adults were observed capturing food, our data include a minimum of 17 adult crows.

Tagged crows were located daily using radio-telemetry and observed from a distance of 2-10 meters, using 8X42 or 10X42 binoculars as needed. The identity of food items and their corresponding stratum and substrate were recorded in descriptive notes. When individuals under observation moved away from the observer, they were not followed. If the observer remained unseen or was able to monitor the bird from a distance, the observation period was extended. Observation sessions ranged from 2-150 minutes with a median of 23 minutes.

Food items were placed into seven categories (defined in Table 2) based on the taxonomy of food items and foraging techniques: 1) adult insects, 2) termite or ant colonies or insect larvae (termites/ants/larvae), 3) *Polistes* wasp nests (wasp nests), 4) lizards, 5) crabs, 6) fruits, seeds and plant materials (fruits/seeds/plants), and 7) Other. Within these categories, many food items were identified further, into sub-categories. Since it was not possible to determine the quantity of some food items, presence/absence of a given category was recorded.

Approximately 10% of observation sessions included a crow taking two or three food items. If multiple food items within an observation were captured from different food categories and/or by different birds and at different locations and times (>10 minutes apart), then food items were treated as independent from one another. If food items were not independent, a single item was selected randomly from those taken in a given 10-minute block. Thus, all tables, figures and statistical analyses display results from independently observed food items.

Forest strata were categorized as ground or above ground (defined in Table 3); foraging substrates (defined in Table 4) were categorized as: 1) dead wood, 2) bark, 3) foliage/branches, 4) rolled leaves, 5) ground debris, and 6) *Pandanus*. *Pandanus* was placed in a separate category from other foliage because foraging crows often target *Pandanus* trees (Jenkins 1983) and use unique foraging techniques to acquire food within them.

Captive-reared Crows

Between December 2013 and November 2014, food items and foraging behaviors were identified during post-release observations of two radio-tagged, captive-reared adult male crows. GU248 (FWS band ID 84477248) was taken in for rehabilitation at 7-months post-fledge and released after one year in captivity. GR010 (FWS band ID 99403010) was taken into captivity on the day he fledged and released after three years in captivity. GR010 was naive to wild foraging prior to his release while GU248 had experience foraging in the wild as a fledgling. The captive crows were released together in an area where wild crows had previously been radio-tracked. Supplemental feedings were provided immediately post-release and tapered according to each individual's need. The mass and body condition of each bird was assessed during opportunistic post-release recaptures. At the completion of data gathering for this study, the captive-reared crows had been tracked for 11 months post-release. Due to the small sample size of captive-reared birds (n=2), we do not make statistical comparisons between the captive-reared and wild crows, but we include it here due to the value of this information for the conservation of the species.

Statistical Analysis

All statistical analyses were conducted using IBM SPSS Statistics 19. Log-linear analysis was not used because the study design is not fully factorial. One of the food categories (crabs) is found only on the ground and this observed relationship between forest stratum and food category violates an assumption of log-linear analysis. We used three Pearson's chi-squared tests to test our hypotheses about relationships between three sets of categorical variables: 1) age class and food category, 2) age class and forest stratum, and 3) season and food category. The analysis of the relationship between age class and forest stratum was conducted both with and without the "crabs" category to determine if adult crows' high rates of crab predation were driving differences in strata-use between age classes.

To control for Type I Error, alpha was set at .05 and a family-wise alpha of .01 was used for the three primary chi-squared tests. We also conducted all pairwise comparisons of food category and age class using additional 2X2 chi-square tests. The Bonferroni correction was applied to pairwise comparisons and alpha was set at .002. We report raw *P*-values for all pairwise comparisons.

Results

Wild Crows

This study identified 619 food items taken by 36 wild crows (Table 5) and determined the corresponding foraging strata and substrates for 469 and 363 items respectively. Fourteen percent of food captures were plant-based foods and 86% were animal prey; 65% of animal prey were insects or their larvae and eggs. Adult insects were the most frequently captured food category within each age class and made up 31% of food items (Figure 1).

Ninety-nine percent of food items were attributed to crows of known age; of those, 33% were attributed to fledglings, 41% to sub-adults, and 26% to adults. Fledglings and sub-adults consumed the food items they procured while adults fed 84% of captured food items to their offspring. Because of this, fledgling food-capture frequencies do not accurately reflect their food intake. Fledglings began to manipulate and explore objects immediately after leaving the nest, however functional foraging was rarely observed during the first month post-fledging. Fledglings dispersed between four and 10 months post-fledging (M = 8 months, n = 13) and the recruitment of one known-age sub-adult into the breeding population occurred at 16 months post-fledging, which is the youngest documented recruitment of a Mariana Crow.

Due to the variation in age at dispersal, there was some overlap in the absolute age (in days post-fledging) between the fledgling and sub-adult categories. The mean (± SD) age of known-age fledglings and sub-adults during observed food captures was 170 ± 68 days (range = 10-293) for fledglings, and 302 ± 66 days (range = 122-462) for sub-adults. Most adults were unbanded and their exact ages were unknown.

Wild crows captured animal prey from all forest substrates accessible to them. Ants, termites, and insect larvae were captured primarily by excavating dead wood; *Polistes* wasp nests were pulled from the undersides of leaves or from small branches, and crabs were located by searching through ground debris. Lizards and adult insects were captured from a variety of substrates (Table 6). Since sufficient descriptions of substrate were absent from 28% of observed food captures, Table 6 represents the minimum numbers of items from each food category taken from each substrate.

We found a strong association between age class and food type, $\chi^2(12, N = 611) = 151.59$, $p < .001$, V=.352 (Figure 2). As predicted, adults captured significantly more crabs than fledglings $\chi^2(1, N = 359) = 34.93$, $p < .001$ or sub-adults $\chi^2(1, N = 411) = 29.75$, $p < .001$, and fledglings took more fruits/seeds/plants than adults $\chi^2(1, N = 359) = 30.80$, $p < .001$ or sub-adults $\chi^2(1, N = 452) = 35.02$, $p < .001$. Based on timed observations of hermit crab predation events, adults spent 3-7 minutes (M = 4.4, n = 6) opening hermit crabs while sub-adults spent 9-24 minutes (M = 17.6, n = 3). Hermit crab predation by fledglings was too rare (n = 1) to quantify in a meaningful way.

Additional pairwise comparisons suggested that fledglings captured more ants/termites/larvae than sub-adults $\chi^2(1, N = 452) = 11.63$, $p = .001$ or adults $\chi^2(1, N = 359) = 32.90$, $p < .001$, and that sub-adults captured more ants/termites/larvae than adults $\chi^2(1, N = 411) = 9.57$, $p = .002$. Fledglings captured fewer adult insects than adults $\chi^2(1, N = 359) = 12.09$, $p = .001$ or sub-adults $\chi^2(1, N = 452) = 17.02$, $p < .001$. Sub-adults trended towards capturing more lizards than fledglings $\chi^2(1, N = 452) = 7.17$, $p = .007$, and more wasp nests than fledglings $\chi^2(1, N = 452) = 5.78$, $p = .016$, however these results were not significant at the level of the Bonferroni-adjusted alpha (P=.002).

There was a moderate association between age class and forest strata, $\chi^2(2, N = 466) = 13.12$, $p = .001$, V=.168 (Figure 3). Pairwise comparisons showed that adults obtained significantly more food from the ground than sub-adults, $\chi^2(1, N = 295) = 13.10$, $p < .001$, and tended to capture more food from the ground than fledglings $\chi^2(1, N = 252) = 4.05$, p =.044. However, when captures of crabs were removed from the analysis, the relationship between age class and foraging strata disappeared $\chi^2(2, N = 435) = 5.28$, $p = .071$, V=.110.

We found no support for the hypothesis of seasonal differences in food category frequencies, $\chi^2(6, N = 531) = 2.51$, $p = .87$. We repeated this analysis for each age class individually, and also after reclassifying food items into three categories: crabs, non-crab animal items, and plant-based items. None of these analyses provided evidence for seasonal differences in food category frequencies.

Captive-reared Crows

Between December 2013 and November 2014 we categorized 209 food items from the two captive-reared crows after release (Table 7); 93 food items were attributed to GU248, and 116 items were attributed to GR010. GU248's last supplemental feeding was on day 19 post-release while GR010's was on day 26. GR010's mass went from 270 grams at release to 266 and 284 grams at 2 and 4.5 months post-release. GU248's mass increased from 274 grams at release to 284 grams at 4 months post-release.

Anecdotally, (Figure 4) the captive-reared crows' food captures were different from wild birds in some respects and they often differed from each other as well. GR010's high percentage of adult insect captures were similar to those of wild sub-adults and adults while GU248's low percentage of adult insects more closely resembled the food captures of the fledgling age class. The captive-reared crows' high percentage of foods from the ants/termites/larvae category was more similar to wild fledglings than other age classes. However, the most notable differences between the captive-reared and wild crows appeared within their consumption of lizards, fruits, and wasp nests. Both captive-reared crows took fewer lizards and fruits and more wasp nests than any age class of wild crow.

The foraging stratum was recorded for 202 of 209 food items; relative frequencies of strata use were within the range of values for age classes of wild crows (Figure 5). GR010 captured food items from the ground 33% of the time and GU248 did so 27% of the time. Wild adults foraged from the ground 41% of the time.

The corresponding foraging substrate was recorded for 176 of 209 food items (Table 8). The captive-reared crows foraged from the same substrates as wild birds. However, wild crows captured at least 49% of their geckos from *Pandanus* trees while the captive-reared crows only captured 12.5% of their geckos from *Pandanus*, taking them instead from rolled leaves, branches and foliage, bark, and dead wood.

Discussion

Like most *Corvus* species, Mariana Crows feed on a wide variety of animal and plant-based foods. We confirmed previous reports that insects, insect larvae, lizards, fruits, and *Coenobita* hermit crabs are common food types and we identified several plant and animal species and one fungus that was not reported previously in the diet of the Mariana Crow. New animal prey items included *Polistes* wasp larvae, *Scolopendra* centipedes, non-*Coenobita* land crabs, and a single observation of a cane toad (*Bufo marinus*) predation in which only the tongue was consumed. The most notable among new plant-based items were fruits of the non-native shrub, *Triphasia trifolia*.

We also observed crows eating foods left by humans for livestock or as bait for wild animals. Crows were seen eating flesh from coconuts that had been opened and tied to the ground by hunters as bait for Coconut Crabs (*Birgus latro*, Table 5). We were told by four different landowners that crows regularly came to their yard to eat coconuts that were left out for livestock. Additionally, two trail cameras took photographs of crows investigating canned fish that was left as bait outside of cat traps (S. Faegre, pers. obs., D. Hartman, pers. comm. 2013).

Mariana Crows foraged in a wide variety of forest substrates, frequently targeting dead or decaying plant material. Adult insects, particularly those in Orthoptera suborder *Ensifera* were often captured from rolled, dead leaves in the understory; ant (Hymentopera) and termite (Isoptera) colonies and insect larvae were excavated from dead wood, using woodpecker-like blows. Lizards (primarily geckos) were commonly captured from a variety of trees, particularly *Pandanus*, and from the ground. Many *Pandanus* trees have high densities of Oceanic Geckos (*Gehyra oceanica*), which are commonly taken by crows (S. Faegre, pers. obs.). Crows foraging in *Pandanus* trees searched through debris that had collected at the bases of the leaves and tugged and tore at smaller leaves, or punctured the bases of leaves, to access hidden prey.

Eighty-seven percent of plant-based foods were fruits taken from trees or shrubs. Fruits were taken from 15 tree species, 13 of which are native to Rota. The three most commonly consumed fruits were from *Triphasia trifolia*, *Artocarpus sp*. and *Carica papaya*. Of these three, only *Artocarpus* is native to the Mariana Islands while *C. papaya* and *T. trifolia* are naturalized. The fruits of *T. trifolia* were consumed more frequently than any other fruit and made up 43% of fruit foraging observations. *Triphasia trifolia* is a common understory shrub within primary and secondary limestone forest. The prevalence of this shrub in crow habitat, along with its prolific, year-round fruiting, might account for the frequency with which it is eaten by crows. Four wild Mariana Crows, taken into captivity for rehabilitation, showed a preference for the fruits of *C. papaya* and *Premna obtusifolia* over *T. trifolia* when given a choice (S. Faegre, pers. obs.).

Animal food sources accounted for 86% of food items captured by Mariana Crows. Fruit was eaten infrequently, especially by sub-adults and adults (Figure 2). Native and introduced fruits were considered a primary component of the diet of wild Hawaiian Crows (*Corvus hawaiiensis*), though they also frequently consumed small invertebrates, bird eggs, and nestlings

(BirdLife International 2013). Hawaiian Crows, currently extinct in the wild, are considered more frugivorous than continental *Corvus* species (BirdLife International 2013) and it is likely that they are also more frugivorous than Mariana Crows. This difference in diet could be important to consider if diets of captive Mariana Crows, and particularly rearing diets for nestlings, are modeled after diets used successfully for captive Hawaiian Crows.

We found no evidence of an effect of season on Mariana Crow food-capture frequencies for any age class, within two different scales of food categorization. While the fruiting of some tree species on Rota is known to increase during the wet season, other trees fruit at high levels in both seasons (Amidon 2000). However, since Mariana Crows eat very little fruit or plant-based items, any differences in tree phenology were unlikely to be reflected by our results. The lack of seasonal effect in this study may reflect a year-round abundance of the crow's primary animal prey. Avian food resources, such as insects, are often more reliable in tropical environments (Karr 1976), as compared to temperate environments.

We found age-related differences in the diets of wild Mariana crows. The frequency of fruits/seeds/plants taken decreased as birds aged, from 29% in fledglings to 8% and 6% in sub-adults and adults. The frequency of predation on ants/termites/larvae also decreased, from 35% to 20% to 9% in fledglings, sub-adults, and adults respectively. Crab predation, on the other hand, increased as birds aged, from 2% and 4% in fledglings and sub-adults, to 20% in adults. The fruits/seeds/plants and ants/termites/larvae categories contain foods that are easier to procure, requiring the repetition of a few, simple movements. Crab capture and processing, on the other hand, requires a complex sequence of movements, culminating in a rapid shaking behavior that is not employed in other types of foraging (S. Faegre, pers. obs.). Overall, prey capture that required the correct sequencing of discrete behaviors, and/or the use of fine motor skills, occurred more frequently in older birds, suggesting that the differences may result from physical maturation and steps in learning.

In this study, Mariana Crow hermit crab processing was comprised of three suites of behaviors: 1) placement of the shell, 2) breaking the shell, and 3) removal of the crab abdomen. The sequence and strategies varied between age classes and individuals, with greater consistency among wild adults. In wild adults, step one was completed quickly, after which crows pecked forcefully at shells, usually directing their blows at suture lines or other weaknesses on the surface. Breaking the shell usually created an access point from which a crow could reach the abdomen, causing the crab to emerge from its shell. When a crab emerged, it was pinched at the joint between the carapace and the abdomen and shaken rapidly from side to side until the abdomen separated (S. Faegre, pers. obs.).

Fledgling Mariana Crows, both wild and captive, watched their parents/mentors closely during crab processing and frequently appeared to imitate their movements. However, they often used processing behaviors in the incorrect order or directed at the wrong part of the crab (S. Faegre, pers. obs.). The crab processing skills of three captive-reared Mariana Crow fledglings developed gradually over a period of 1-2 years. Similarly, New Caledonian Crows (*Corvus moneduloides*) rely on a combination of social learning and trial and error for the development of larva fishing behavior and do not become proficient at larva-fishing with stick tools until they reach at least one year post-fledging (Bluff *et al*. 2010; Holzhaider *et al*. 2010a,b). Other corvid species, including the Common Raven (*Corvus corax*), have also demonstrated the ability to use social learning to acquire a novel foraging behavior in a captive setting (Fritz and Kotrschal 1999). It is likely that both trial-and-error and social learning are needed for the acquisition of crab handling behaviors in Mariana Crows.

Island endemic animals often have reduced vigilance behaviors compared to mainland species due to relaxed selection for anti-predator traits in predator-depauperate environments (Blumstein 2002, Blumstein *et al.* 2004). The island endemic New Caledonian Crow rarely scans the sky for predators while foraging on or near the ground (Rutz & St. Clair 2012). Similarly, Mariana Crows sometimes failed to detect an approaching human observer while processing food items low or on the ground (S. Faegre, pers. obs.). The Mariana Crow evolved without any natural predators and may have been subject to relaxed selection for anti-predator behaviors during this time. While Mariana Crows respond appropriately when they see a predator (e.g. feral cat), their apparent lack of vigilance behaviors may make them particularly vulnerable to feral cat predation during the time it takes them to subdue and process hermit crabs on the ground.

The Mariana Crow's frequent predation of *Coenobita* hermit crabs is unique among *Corvus* species and among most land birds. In particular, the Mariana Crow's method of opening hermit crab shells by pounding on them repeatedly, rather than dropping them on a hard surface, is rare. Only two species of flightless rail, the Aldabera White-throated Rail (*Dryolimnas cuvieri aldabranus*) and the extinct Wake Island Rail (*Gallirallus wakensis*) are known to open hermit crab shells by pecking them open on the ground (Wanless & Hokey 2008, Olson & Rauzon 2011). Many *Corvus* species habitually crack hard-shelled food items, such as nuts, by dropping them on hard surfaces (Cristol & Switzer 1999, Hunt *et al*. 2002); however this behavior has only been observed once in the Mariana Crow (T. San Nicholas, pers. comm., 2014).

There are five species of *Coenobita* hermit crab on Rota. Four of these, *C. brevimanus*, *C. spinosus*, *C. cavipes* and *C. perlatus*, are commonly found in crow habitat while the fifth, *C. rugosus*, is found mainly on shores. *Coenobita brevimanus* is the most common species within the limestone forests of Rota and is also the most commonly depredated by crows (S. Faegre, pers. obs.). *Coenobita* species in forested areas of Rota use primarily Giant African Land Snail (*Achatina fulica)* and *Turbo sp.* shells. Shells from the introduced *A. fulica* are relatively weak and are almost exclusively the shell-type observed among crabs that are depredated by crows. The harder *Turbo sp.* sea snail shells are native to Rota. Although there have been two observations of crows removing *Coenobita* hermit crabs from *Turbo* shells, neither observation involved the crow breaking the shell (H. Fandel, pers. comm. 2014).

The introduction, subsequent invasion and then control of *A. fulica* on Rota may have indirectly impacted Mariana Crows due to the effects of shell type and availability on *Coenobita* hermit crabs. *Achatina fulica* was introduced to the Mariana Islands as a food source between 1936 and 1938 where it became a major agricultural pest. Attempts to control it began in 1950 (National Research Council U.S. 1954), but it was not until the establishment of the flatworm (*Platydemus manokwari*) in the late 1970s that the population was dramatically reduced (Nafus & Schreiner 1989). The combination of high densities of *A. fulica* followed by effective control may have led to an increase in shell availability, and subsequently an increase in weak-shelled hermit crabs for crows. An increased availability of *Coenobita* hermit crabs, which are rich in nutrients and high in fat (Lawrence 1976), may have been beneficial to the crow population.

However, given recent data suggesting that feral cat predation is a cause of mortality for Mariana Crows (S. Faegre and R. Ha unpublished data), a historical increase in crab predation could also have carried risks. In this study, adults captured more food items from the ground than other age classes, entirely due to their increased frequency of hermit crab predation. Whether this higher frequency of ground-based food captures in adult crows means that adults also spend more time foraging on the ground than other age classes, however, is unclear. On average, sub-adults took four times longer than adults to break open hermit crab shells; they were also observed making unsuccessful attempts at crab predation while adults never failed to open a crab. Young fledglings followed their parents closely during foraging, especially when food was being processed (S. Faegre, pers. obs.), and the time they spend on the ground may mirror that of their parents. An increase in crab availability after the control of *A. fulica* may have led to an increase in ground-based foraging behaviors for crows of all ages. A study comparing ground-based foraging time budgets for each age class would help clarify age-based vulnerabilities.

The two captive-reared crows in this study became independent of supplemental foods less than one month post-release, and at four months post-release both crows were recaptured in good body condition, each with a mass about 10 grams heavier than their pre-release mass. Our comparisons of diet and foraging behavior of wild and captive-reared crows were encouraging overall, in that the captive-reared crows foraged successfully on all prey types common in the diets of wild crows. The captive-reared crows also foraged differently from wild crows in some ways. Their high frequencies of wasp nest predation and low frequencies of fruit and lizard predation, for example, have several possible explanations. In captivity, crows were given geckos, hermit crabs, mice, and fruits on a daily basis. Wasp nests and/or insects were given less frequently, approximately once per 1-2 weeks, and were always preferred over more common food items (S. Faegre, pers. obs.). After their release, the captive crows may have sought out their preferred foods (wasp nests and insects) and had lower levels of motivation to forage for geckos or fruits.

Alternatively, they may have lacked the skills to locate fruits and capture geckos in the wild, due to a paucity of realistic gecko- and fruit-foraging opportunities in their captive environment. While realistic wasp nest foraging opportunities were not presented in captivity, the reinforcement of the wasp nest search image appears to have been sufficient preparation for the naive, captive-reared GR010 to successfully capture a wasp nest during his first encounter with this item in the wild (S. Faegre, pers. obs.). Wasp nest predation, while potentially dangerous, does not require specialized skills. GR010's infrequent lizard captures, both compared to wild crows and to GU248, the partially wild-reared member of his cohort, suggest that a search image alone may have been inadequate for GR010's development of lizard capture skills. Live geckos were presented to the captive crows, but infrequently and not in a natural foraging environment. Since wild crows capture most of their geckos from *Pandanus* trees, we recommend providing increased opportunities for captive crows to hunt live geckos in *Pandanus* trees.

While this study's foraging data suggest that the captive-reared crows' ground-based food capture rates were within the normal range for wild crows, more general behavioral observations indicated that the duration of ground-based activities overall were higher in the released crows than wild crows (S. Faegre, pers. obs.). GR010, in particular, spent excessive periods of time on the ground during the first 2-3 months post-release, and was not observed flying above the canopy during the first seven months post-release. Upon release, an unpaired adult female frequently followed either GR010 or GU248 in ground-based activities including, most notably, lengthy periods of travel by hopping and walking along the ground, rather than flying from tree to tree. The excessive duration of ground-based activities in the released crows declined over time and, at nine months post-release, no differences in strata use between the released and wild crows were observed (A. Kroner, pers. comm. 2014). Due to the presumed increased risk of cat predation for crows on the ground, increasing the canopy-based enrichment opportunities within aviaries could be beneficial. Additionally, due to the well-documented potential for social transmission of behaviors in corvids and other birds (Fritz & Kotrschal 1999, Slagsvold and Wiebe 2011, Auersperg *et al*. 2014), the potential for atypical behaviors of released Mariana Crows to affect the behavior of wild crows should be considered.

With a sample size of two released birds, we cannot rule out the possibility that observed differences between wild and captive-reared crows were caused by individual preferences or other factors unrelated to their rearing environment. Additional data from future releases of captive-reared crows will provide further insight into the effects of captive-rearing on behavior.

While the results presented here begin to answer questions about Mariana Crow diet and foraging behavior, there are limitations. The Mariana Crow occurs at extremely low densities and it was impractical to follow a sampling regimen that allowed equal sampling of strata, individuals, or habitats. Known individuals could not be represented equally in the data due to different lengths of tracking (due to mortality), variations in visibility due to forest density, and variations in the tolerance of individuals to human presence. Therefore, the results may be biased towards birds that were bolder, longer lived, and which occupied forests with greater visibility. Additionally, due to the opportunistic nature of the observations, it is likely that our data were biased towards larger food items with longer handling times, especially during observations of adults with offspring, which often kept a greater distance between themselves and human observers while foraging. Wild, radio-tagged adults, in particular, yielded very few foraging observations due to their frequent intolerance of human observers (S. Faegre, pers. obs.). At the other extreme, the captive-reared crows and wild sub-adult crows had little apparent reaction to the proximity of humans.

The possibility of individual specialization in foraging strategy could not be investigated in this study due to the low number of observations per known individual. A future study that incorporates individual identity into the analysis would provide an interesting additional dimension to this study.

Conclusions

Our primary recommendations, based on behavioral observations of the two released crows are that, a) increased opportunities for captive crows to hunt live geckos and consume a variety of whole, native fruits, presented as naturally as possible, could increase their post-release proficiency with these food types, and b) a large, flight aviary would provide opportunities for captive crows to travel longer distances at canopy height and may decrease excessive ground-based activities after release.

Mariana Crows show evidence of age-related differences in diet and foraging behavior that are likely driven by motor maturation and learning during the fledgling and sub-adult life stages. Predation of hermit crabs may put crows at higher risk for feral cat predation, due to increased time spent foraging on the ground. Very little is known about the foraging behaviors of other tropical Asian/Australasian crows that are likely candidates for hermit crab predation behaviors; observations of these species could lead to a better understanding of crab-foraging behaviors in the absence of *A. fulica* shells.

In this study, we have shown that Mariana Crows of all ages captured nearly one third of their food items from the ground and that adults captured significantly more food items from the ground than other age classes due to their frequent capture hermit crabs. We have also noted that Mariana Crows evolved on a predator-free, oceanic island and that while foraging low or on the ground they can fail to detect an approaching observer, indicating that they may have reduced vigilance behaviors, compared to mainland *Corvus* species. The fact that Mariana Crows forage on the ground for much of their sustenance underscores the importance of continuing a program of feral cat control.

Figures

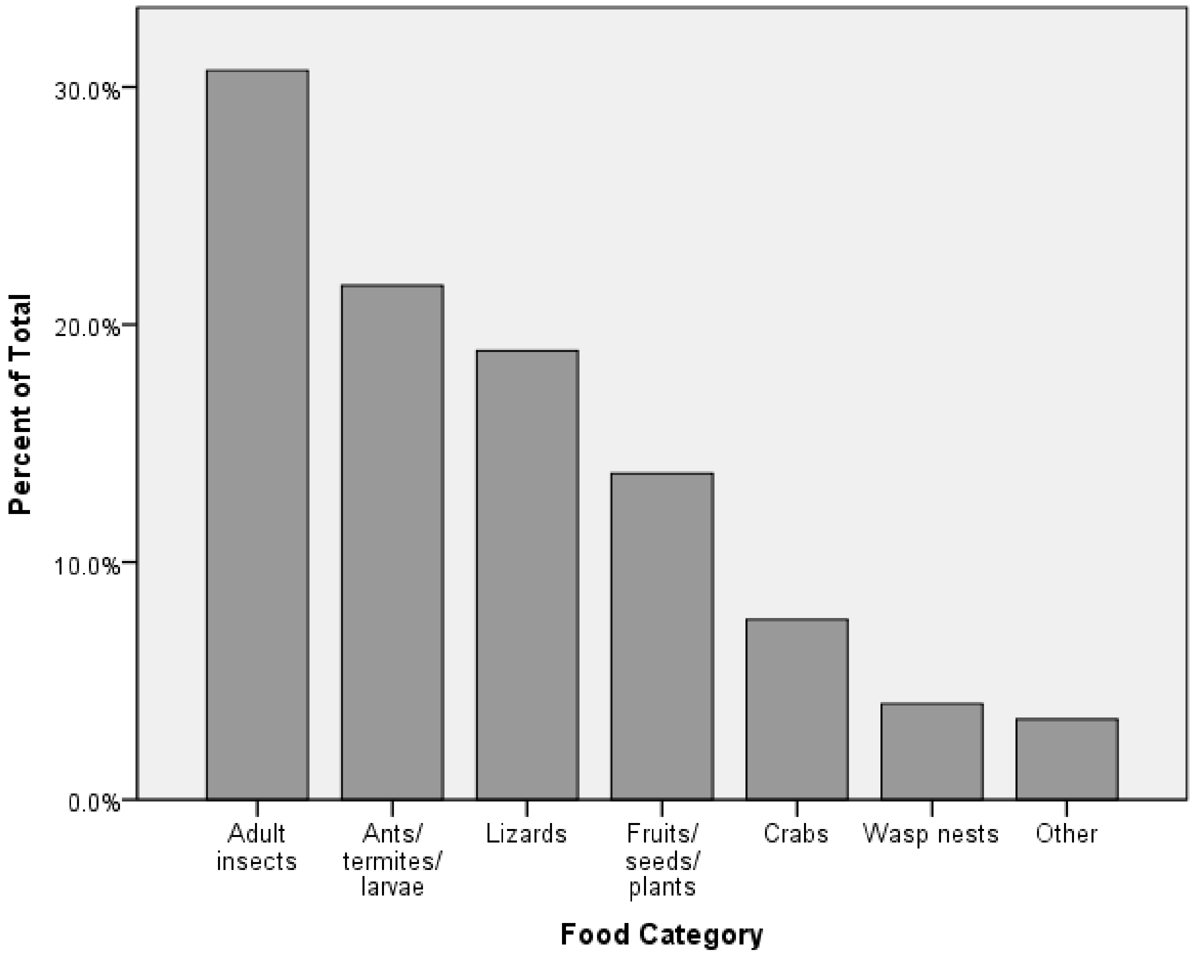

Figure 1.1: Frequency distribution of food categories for all ages combined

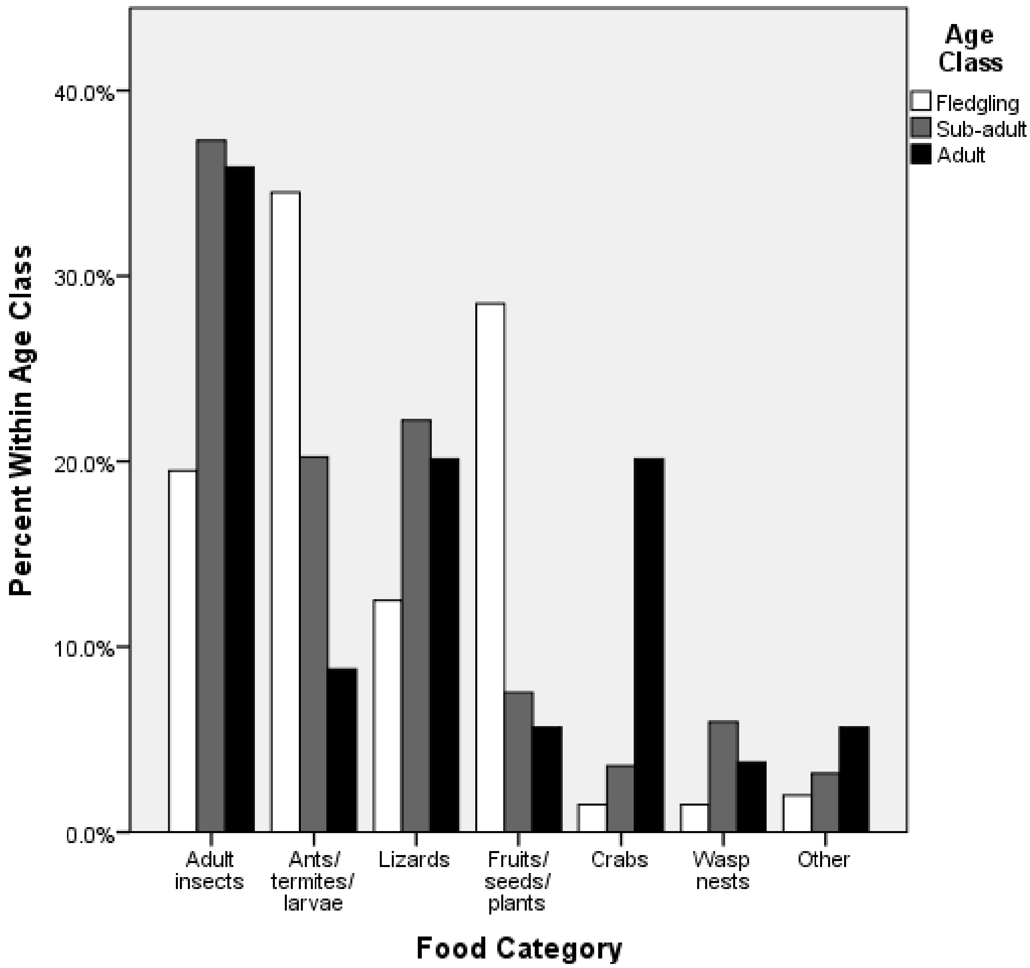

Figure 1.2: Percentage of food categories captured by wild fledglings, sub-adults, and adults

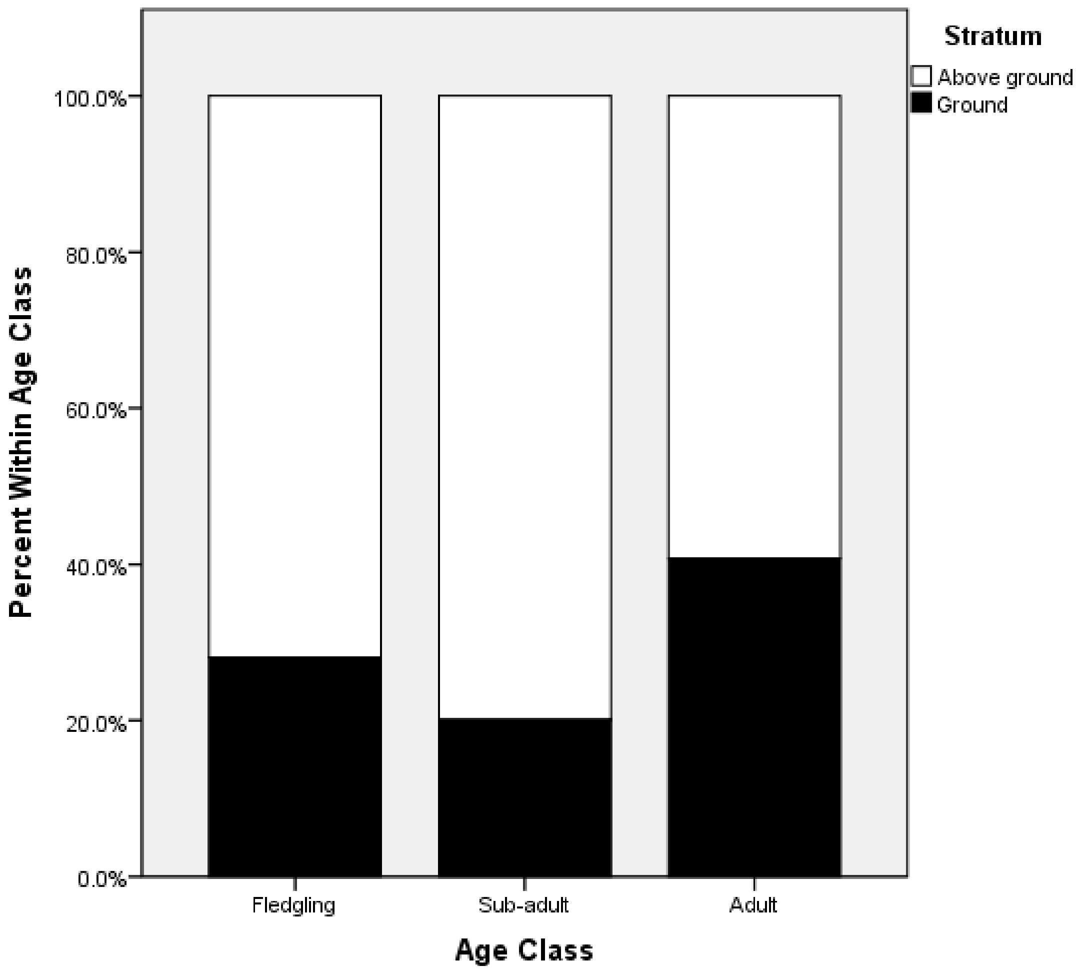

Figure 1.3: Percentage of food items captured from ground vs. above ground by wild fledglings, sub-adults, and adults

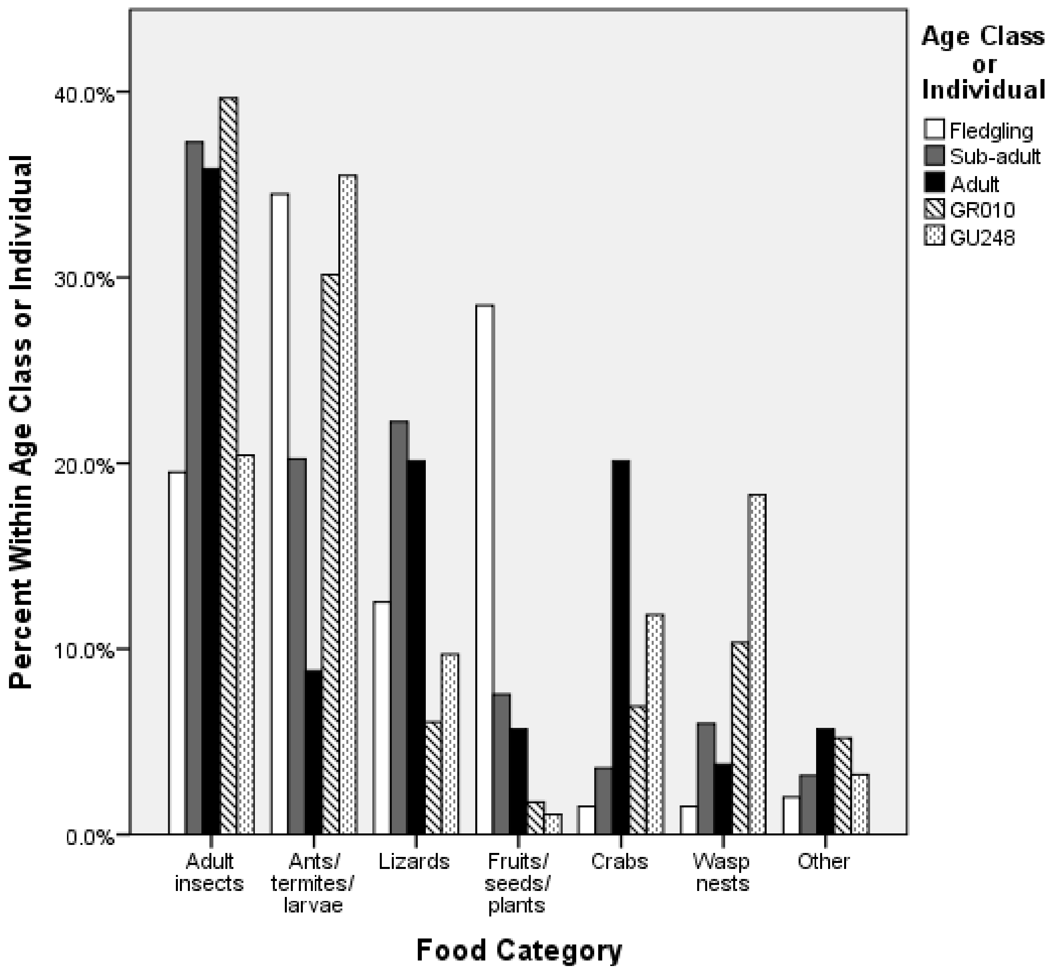

Figure 1.4: Percentage of food categories captured by wild and captive-reared crows

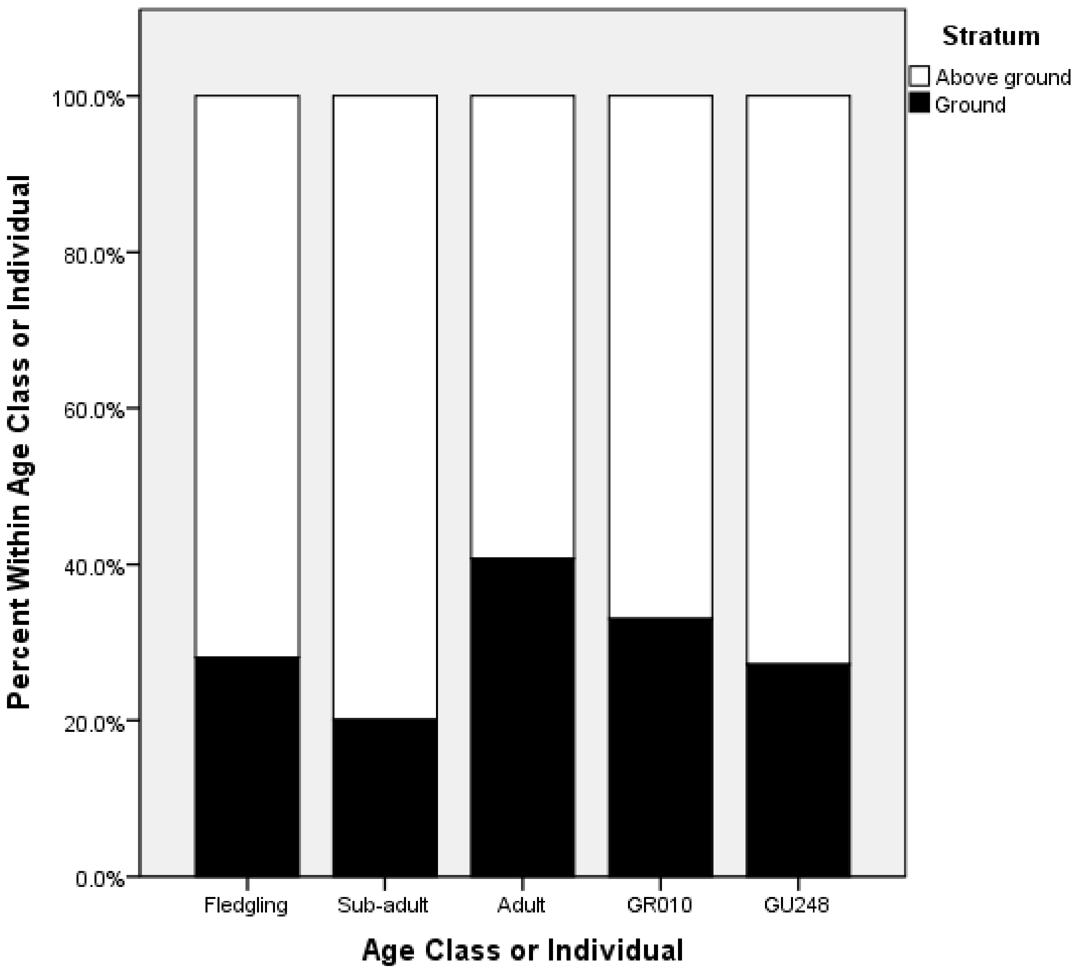

Figure 1.5: Percentage of food items captured from ground vs. above ground by wild and captive-reared crows

Tables

Table 1.1. Mariana Crow age class definitions

Fledgling	From fledge date until nutritional independence from parents (mean= 8 months; Morton *et al*. 1999)
Sub-adult	From nutritional independence from parents until the first date observed nesting
Adult	From the first date observed nesting until death

Table 1.2. Mariana Crow food category definitions

Adult insects	All adult insects except those belonging to Isoptera: *Termitoidae* or Hymenoptera: *Formicidae*
Termite or ant colonies or insect larvae (termites/ants/larvae)	Adults insects belonging to Isoptera: *Termitoidae* and Hypenoptera: *Formicidae* and larvae or eggs of any insect
***Polistes* wasp nests (wasp nests)**	*Polistes* wasp larva
Lizards	Animals of the suborder *Lacertilia*
Crabs	Animals of the order *Brachyura*
fruits, seeds and plant materials (fruits/seeds/plants)	Fruits, seeds, foliage, bark, and any other plant material
Other	Bird eggs or nestlings, lizard eggs, fungi, amphibians, and arthropods not belonging to *Brachyura* or *Insecta*

Table 1.3. Mariana Crow foraging strata definitions

Ground	On the forest floor or less than one foot from the forest floor (e.g. fallen logs)
Above ground	More than one foot above the forest floor

Table 1.4. Mariana Crow foraging substrate descriptions

Dead Wood	Rotten wood, either fallen or in a snag or live tree; crows excavate animal prey by tearing and/or pecking.
Bark	Dead or live bark, peeled or flaked from trees to find hidden prey, or to eat live bark.
Foliage/branches	Food items gleaned directly from branches/twigs or foliage of any plant except *Pandanus* species.
Rolled leaves	Dead or live, rolled/crumpled leaves; can be growing from a tree but are usually fallen leaves, caught in the branches/foliage of trees and shrubs. Prey is initially partly or fully hidden inside a rolled leaf.
Ground debris	Food item picked up from the ground or uncovered by moving debris (leaves, twigs, chunks of rotten wood) with the bill, or pulling prey from a crevice between rocks or roots.
Pandanus sp.	Food item taken from live or dead *Pandanus* species, including debris accumulated in their crowns.
Substrate not observed	Observer did not see what substrate the food item was taken from.
Substrate not recorded	Insufficient data were recorded to categorize substrate.

Table 1.5: Food items taken by wild Mariana Crows

Adult Insects (except *Termitoidae* or *Formicidae*)	**#**	**Sub-totals**
Ensifera sp. (Crickets and Katydids)	**103**	
Mantodea sp. (Mantids)	**3**	
Phasmatodea sp. (Walkingsticks)	**1**	
Lepidoptera sp. (Moths and Butterflies)	**1**	
Unknown adult insect	**82**	
		190
***Termitoidae* or *Formicidae* Colonies and Unknown Insect Larvae or Eggs**		
Termitoidae or *Formicidae* colony (unspecified)	**56**	
Formicidae (ant) colony	**23**	
Termitoidae (termite) colony	**4**	
Lepidoptera (moth/butterfly) larvae	**3**	
Unknown insect egg case	**3**	
Unknown insect larvae	**45**	
		134
***Polistes* (wasp) Nests**		
		25
***Lacertilia* (lizards)**		
Lacertilia sp.		**5**
Gekkonidae sp. (Geckos)		**103**
Scincidae sp. (Skinks)		**9**
		117
***Brachyura* (Crabs)**		
Coenobita sp. (Hermit crabs)	**43**	
Birgus latro (Coconut crabs)	**1**	
Other land crabs	**3**	
		47
Fruits, seeds and other plant-based items		
Artocarpus sp. Fruit	**11**	
Carica papaya fruit	**8**	
Cocos nucifera fruit	**4**	
Cordia subcordata fruit	**2**	
Eleocarpus joga fruit	**1**	
Eugenia sp. Fruit	**2**	
Ficus sp. Fruit	**1**	
Guamia mariannae flowers	**1**	
Hernandia sp. fruit	**1**	
Intsia bijuga bark	**2**	
Melanolepis multiglandulosa fruit	**1**	
Mammea odorata leaf stems	**1**	
Mucuna sp. seed	**2**	
Ochrosia mariannensis fruit	**1**	
Pipturus argenteus fruit	**4**	
Premna obtusifolia fruit	**2**	
Psychotria mariana fruit	**2**	
Scaevola sercea fruit	**1**	
Triphasia trifolia fruit	**32**	
Unknown fruit	**5**	
Unknown seed	**1**	
		85
Other		

Aplonis opaca (Micronesian Starling) nestling	**3**	
Gallicolumba xanthonura (White-throated Ground Dove) nestling	**4**	
Gygis alba (White Tern) egg	**1**	
Rhipidura rufifrons (Rufous Fantail) nestling	**1**	
Unknown nestling	**3**	
Bufo bufo (Cane toad)	**1**	
Araneae sp. (Spider)	**3**	
Scolopendra sp. (Centipede)	**2**	
Lacertilia sp. (lizard) eggs	**2**	
Aricularia sp. mushroom	**1**	
		21
Grand Total		**619**

Table 1.6. Frequencies of foraging substrates within food categories taken by wild Mariana Crows

	Adult insects	**Termites/ants/ larvae**	**Wasp nests**	**Lizards**	**Crabs**	**Fruits/seeds/ plants**	**Other**	**Total**
Dead Wood	2	87	0	0	0	0	0	**89**
Bark	2	6	0	0	0	2	0	**10**
Foliage/branches	12	5	6	3	0	62	2	**90**
Rolled leaves	33	3	0	2	0	0	0	**38**
Ground debris	16	4	0	10	34	11	1	**76**
Pandanus sp.	12	3	3	41	0	0	1	**60**
Substrate not observed	35	4	11	34	13	3	13	**113**
Substrate not recorded	78	22	5	27	0	7	4	**143**
Total	**190**	**134**	**25**	**117**	**47**	**85**	**21**	**619**

Table 1.7: Food items taken by captive-reared Mariana Crows

Adult Insects (except *Termitoidae* or *Formicidae*)	**#**	**Sub-totals**
Ensifera sp. (Crickets and Katydids)	**43**	
Scoliidae sp. (Scoliid wasps)	**3**	
Lepidoptera sp. (Moths and Butterflies)	**1**	
Unknown adult insect	**18**	
		65
***Termitoidae* or *Formicidae* Colonies and Unknown Insect Larvae or Eggs**		
Formicidae sp. (ant) colony	**44**	
Termitoidae sp. (termite) colony	**12**	
Unknown insect egg case	**7**	
Unknown insect larvae	**5**	
		68
***Polistes* (wasp) Nests**		
		29
***Lacertilia* (lizards)**		
Gekkonidae sp. (Geckos)		**16**
		16
***Brachyura* (Crabs)**		
Coenobita sp. (Hermit crabs)	**18**	
Birgus latro (Coconut crabs)	**1**	
		19
Fruits, seeds and other plant-based items		
Pipturus argenteus fruit	**1**	
Triphasia trifolia fruit	**2**	
		3
Other		
Gallus gallus (Red Junglefowl) eggs	**3**	
Todiramphus chloris (Collared Kingfisher) adult	**1**	
Araneae sp. (Spider)	**3**	
Lacertilia sp. (lizard) eggs	**2**	
		9
Grand Total		**209**

Table 1.8. Frequencies of foraging substrates within food categories taken by captive-reared Mariana Crows

	Adult insects	**Termites/ants/ larvae**	**Wasp nests**	**Lizards**	**Crabs**	**Fruits/seeds/ plants**	**Other**	**Total**
Dead Wood	0	45	0	1	0	0	1	**47**
Bark	2	3	0	1	0	0	0	**6**
Foliage/branches	2	5	27	3	0	2	2	**41**
Rolled leaves	35	2	0	5		0	1	**43**
Ground debris	9	2	0	0	18	1	3	**33**
Pandanus sp.	1	1	1	2	0	0	1	**6**
Substrate not observed	1	0	1	3	1	0	1	**7**
Substrate not recorded	15	10	0	1	0	0	0	**26**
Total	**65**	**68**	**29**	**16**	**19**	**3**	**9**	**209**

Chapter 2: Spatial Ecology of the Mariana Crow: A Radio-tracking Study

Introduction

Animal movement patterns result from a dynamic interplay between individuals and their environment as they perform the behaviors needed to survive and reproduce (Burt 1943). The restriction of activities to a home range can facilitate the exploitation of resources, such as food and nesting areas, while nomadic movement patterns may be advantageous when resources are widespread or highly unpredictable (Börger *et al.* 2008). Intraspecific variation in home range and movements often relate to habitat variables, as well as the density of competing conspecifics, and the age, sex, and social status of the individual (Sanderson 1966, Maher & Lott 2000, McLoughlin & Ferguson 2000, Jetz *et al.* 2004, Kjellander *et al.* 2004, Mitchell & Powell 2004, López-Bao *et al.* 2014). Temporal scale of study is also critical to consider since this can affect the apparent size and structure of home ranges, particularly if home ranges are dynamic (Gautestad & Mysterud 1995, Rolando 2002, Schwarzkopf and Alford 2002, Börger *et al.* 2008, Martinez-Miranzo *et al.* 2016). Identifying factors that influence space use decisions by animals is important for wildlife management (Chalfoun & Martin 2007, Xu *et al.* 2009, Gerber *et al.* 2012) and yet these data are lacking for many endangered species (Rechetelo *et al.* 2016).

The Mariana Crow (*Corvus kubaryi*) is a critically endangered forest bird that faces a high risk of extinction (Ha *et al.* 2010). The crow is endemic to the islands of Rota and Guam but was extirpated from Guam in the 1990s due to predation by the introduced Brown Tree Snake (*Boiga irregularus*; Savidge 1987). The single remaining population of Mariana Crows is confined to the island of Rota and consists of fewer than 200 individuals (Zarones *et al.* 2012;

Kroner & Ha 2017). Theories for the decline of crows on Rota include habitat loss and degradation, persecution by humans, predation and competition from introduced species, and inbreeding depression (Morton *et al*. 1999, Plentovich *et al*. 2005, USFWS 2005, Wiewel *et al*. 2009, Sussman *et al*. 2015). Little evidence is available to support the theories, although recent evidence from radio-telemetry studies suggests that predation from feral cats (*Felis catus*) is an important cause of mortality (S. Faegre and R. Ha, unpublished data).

During the 1990s, habitat removal and degradation from human causes and typhoons were linked to the loss of territorial pairs and reduced nest success (Morton *et al.* 1999, Zarones *et al.* 2015). Habitat loss and degradation continue to impact crows to some degree (e.g. disturbance due to the illegal removal of trees, S. Faegre, pers. obs.), but it is unlikely that this is a limiting factor for population recovery. Knowledge of Mariana Crow spatial behavior is important for the management of remaining Mariana Crow habitat.

While habitat occupancy of Mariana Crows on Rota has been broadly delineated (Zarones *et al.* 2015, Faegre *et al.* 2016, Kroner & Ha 2017), little is known about the home range and movement patterns of the species, and intraspecific differences in home range have never been studied. Previous research, based on opportunistic observations of color banded individuals, suggested that the average home range of Mariana Crow family groups during the fledgling period was 64 ha. and that the density of breeding pairs was approximately one pair per 22 ha. of forested area (Morton *et al.* 1999). In this study, we followed radio-tagged crows to more accurately estimate home range characteristics of the species and to begin to understand how other factors, such as age class and physical development, may relate to differences in movements and home range. Intraspecific differences in mobility have implications for energy expenditure and may indicate different needs or susceptibilities among these groups that could be addressed by managers.

In addition to estimating home ranges during the fledgling and sub-adult life stages, we studied weekly and monthly ranges and daily movements, and generated home range data-area curves, in order to better understand the behavioral processes governing home range behavior (Maher & Lott 2000, McLoughlin & Ferguson 2000). Home range area curves estimate home range area on the Y-axis over increasing numbers of relocation points on the X-axis. Area curves are useful for determining the number of relocation points needed to fully reveal home ranges and can also be indicative of home range stability (Haines *et al.* 2009).

The stability of sub-adult populations directly impacts breeding populations (Penteriani *et al.* 2011), and is particularly important to consider for species with a prolonged juvenile period (Webb *et al.* 2009) or with high adult mortality rates, such as the Mariana Crow (Ha *et al.* 2010). Mariana Crows are not cooperative breeders and, during nesting, pairs defend temporary territories around active nests, excluding conspecifics, including offspring from prior years. After natal dispersal, and prior to being recruited into the breeding population, sub-adult Mariana Crows are rarely seen and their behavior has never been described. In this study, we radio-tracked sub-adults during their first 2-12 months post-fledging and described their social and spatial behaviors.

In this work, we present descriptive statistics on home range size, overlap, and stability, as well as on daily movements during the fledgling and sub-adult life stages. Current habitat management practices for the Mariana Crow population assume that addressing threats near active nests will provide protection in habitat that is most critical to the crow population.

However, a better understanding of Mariana Crow home ranges and movement patterns during the non-nesting period will help determine if the current management strategy is sufficient.

Methods

Study area

Rota is the second most southerly island after Guam in the Mariana Islands, Western Micronesia (14°09'N, 145°12'E). The 85-km^2 island is volcanic in origin with uplifted limestone terraces. The climate is tropical, with high humidity. Wet and dry seasons are typically from July-November (wet) and January-May (dry) with rainfall measuring from a minimum of 3.69 inches/month in March to a maximum of 13.37 inches/month in September (Lander & Guard 2003). Rota is located within the Western Pacific typhoon belt and experiences typhoons periodically.

Radio-tracking

Between March 2010 and January 2017, Mariana Crows were radio-tagged and tracked using Holohil RI-2CT VHF transmitters. Transmitter/harness packages were 3-4% of the body weight of each crow and were fitted to individuals using a backpack design with a weak link system incorporated. All crows in this study were classified as either fledglings or sub-adults. Due to their movements as family units, fledgling movements approximated the movements of their parents during this same time period.

Nutritional independence of young from the parents, at an average age of eight months post-fledging (Morton *et al.* 1999, S. Faegre, unpublished data), generally coincides with dispersal from the natal territory. Crows were classified as fledglings during the period of nutritional dependence on their parents, and as sub-adults after reaching independence from their parents but prior to their first nesting attempt. During daily or bi-weekly observations, tagged crows were observed and social interactions were recorded to determine breeding and social status.

This study included 20 Mariana Crows; 17 were tagged as fledglings, shortly before or after fledgling, and three were tagged as sub-adults of unknown age. When siblings were radio-tagged, only one sibling from the pair was used in each analysis to avoid pseudoreplication. Crows were tracked until death or until failure of the radio-tag. Five crows died prior to natal dispersal (four due to probable feral cat predation) and four had transmitter batteries fail prior to dispersal. The remaining eight crows were tracked through natal dispersal, and tracked as sub-adults for periods of two months to one year.

Home Range Analysis

We used the fixed K local convex hull method (Getz & Wilmers 2004) to characterize home ranges from full data sets (consisting of a minimum of 120 data points), and the minimum convex polygon method (Samuel & Fuller 1994) for analyses of data sets at smaller temporal scales. While there are biological and statistical disadvantages to the minimum convex polygon method when samples are large (Samuel & Fuller 1994), this method is commonly reported and tends to be more robust with smaller numbers of relocation points. We chose the local convex hull (LoCoH) method over kernel density estimators because the LoCoH method represents space use more accurately within landscapes characterized by sharp topographical features and fragmented habitats (Getz & Wilmers 2004, Getz *et al.* 2007). Furthermore, unlike kernel-based methods, the fixed K LoCoH is robust to changes in the smoothing parameter (Getz *et al.* 2007), reducing the potential for biased results and improving the accuracy of inter-individual comparisons. All home ranges were measured at the 100% isopleth.

When possible, we present descriptive statistics for home range size of complete datasets for biologically meaningful life stages (e.g. fledgling period, sub-adult period). However, due to incomplete datasets for the sub-adult period, we used three shortened temporal scales (30, 60, and 90 days post-fledging or post-dispersal) when testing for differences between fledgling and sub-adult home ranges.

We evaluated daily mobility among fledglings and sub-adults using daily movement distances (i.e. the distance between daily observations). Home range area curves were used to determine if individual home range boundaries were stable and to determine the number of locations needed to accurately estimate home range size.

Statistical Analyses

All analyses comparing fledgling and sub-adult spatial behavior were done using linear mixed effects models in R (package *nlme*; Piniero & Bates 2017). To satisfy model assumptions, home range area was square-root transformed whenever it was used as a dependent variable and daily movement distance was cube-root transformed. Home range area and overlap were calculated using Reproducible Home Range package in R (Signer & Balkenhol 2015) and ArcView 10.1.

We used two methods to determine the average length of time it took fledglings to reach full mobility. First, we calculated the mean number of days it took fledglings to reach their own mean post-fledging daily movement distance. Second, we visually evaluated the daily movement distances of fledglings over time using the graph from the model for daily movements by weeks post-fledging.

To further explore the stability of fledgling and sub-adult home ranges over the study period we created home range area curves for each individual, beginning either at fledge day or dispersal day, using program BIOTAS 1.0.1a (Ecological Software Solutions 2002), and Excel. We examined area curves visually to see if cumulative areas appeared to approach asymptotes over time.

Results

When analyzing full datasets, home range estimates were 86% higher when using the MCP method, as compared to the LoCoH method. Despite the shorter radio-tracking periods for sub-adults, sub-adult home ranges were 316% larger than fledglings with the MCP method and 167% larger with the LoCoH method (Table 1). Home range overlap between neighbors (directly adjacent and non-adjacent), and sibling pairs (fledgling and sub-adult) are presented in Table 2.

Over 90-day periods, cumulative home range area was larger for sub-adults than for fledglings (F (1, 22) = 9.3668, $p = 0.0057$, Figure 1). Home ranges also increased in area over time, (F (1, 46) = 59.3646, $p < 0.0001$, Figure 1), suggesting that either home ranges were shifting over smaller time periods, or that movements were increasing over time such that birds were using larger areas.

With all fledgling data included, daily movement distances were longer for sub-adults than for fledglings (F (1, 18) = 73.903, $p < 0.0001$) and increased with week (F (1, 477) = 127.686, $p < 0.0001$, Figure 2). There was also a significant interaction between age and week (F (1, 477) = 4.505, $p < 0.0343$). However, these effects were driven primarily by low mobility during the early post-fledging period. After removing the first ten weeks post-fledge there was a marginally significant effect of age (F (1, 18) = 4.100, p = 0.0580, Figure 3), but neither the interaction (F (1, 359) = 0.453, p = 0.5013) nor the effect of week (F (1, 359) = 1.440, p = 0.2309) was significant.

Non-cumulative home range size increased with age (F (1, 22) = 22.8136, $p < 0.0001$) and month (F (1, 107) = 14.8724, $p < 0.0002$, Figure 4). After removing the first month post-fledge and re-analyzing the data, the effect of age remained (F (1, 22) = 8.5859, p = 0.0077), but the effect of month was no longer significant (F (1, 90) = 0.0767, p = 0.7824). With all data included, percent overlap was significantly larger for sub-adults than for fledglings (F (1, 22) = 4.4521, p = 0.0465, Figure 5) suggesting that, opposite to our predictions, fledgling home ranges shifted more than sub-adults. Percent overlap also increased with month (F (1, 84) = 33.3951, $p < 0.0001$, Figure 5). Re-analyzing the data after removing the first month post-fledging eliminated the significant effect of age (F (1, 22) = 0.2772, p = 0.6038), but the effect of month remained (F (1, 67) = 8.5308, p = 0.0048). This suggests that fledglings, traveling with family groups, as well as sub-adults, have dynamic, shifting home ranges that lack stable boundaries. The effect of month suggests that initial shifts away from the nesting area were larger than shifts over subsequent months.

It took a mean of 31.4 days (SD = 9.13, n = 14) for fledglings to reach their own average daily movement during the fledgling period. However, visual examination of daily movement distances (Figure 2) suggested that it may take 10 weeks for fledglings to maintain average levels of mobility.

Home range area curves showed that most fledglings and sub-adults continued to expand into new areas over the study period and lacked home ranges with stable boundaries (Figures 6-

8). This prevented a meaningful analysis on the minimum number of points needed to accurately estimate home range size, as area continued to increase over the entire study period.

Discussion

The home range estimates for Mariana Crow family groups in this study (76 and 53 hectares for MCP and LoCoH respectively) were similar to Morton *et al.*'s (1999) estimate of 64 hectares. During 30, 60, and 90-day periods, sub-adult Mariana Crow home ranges were more than twice the area of fledglings (84.03 ha vs. 38.33 ha). This difference is not likely attributed to mobility since the first 31 days post-fledgling were removed from the data set for this analysis. In general, dispersing sub-adult birds often lack stable home ranges and spend periods of time moving nomadically, in search of resources or breeding territories (Penteriani *et al.* 2011). Sub-adult Mariana Crows may be using large areas after dispersing from their natal territories for a number of reasons, including an increase in exploratory behavior, a need to roam more widely to find resources without intruding on areas occupied by breeding individuals, or a need to travel large distances to find unpaired conspecifics or vacant nesting habitat.

While measures of total home range area over meaningful biological periods (such as the fledgling period) are important for understanding habitat needs of a species, some authors question the use of the home range asymptote as a neutral model for home range analysis. Instead, it has been proposed that a multiscale home range concept, which has fractal properties and is not expected to reach an area asymptote (Gautestad & Mysterud 1995), may be more appropriate for understanding home range movement processes. Mariana Crow home ranges, when measured cumulatively, increased over time. However, when home range areas were measured in 30-day sequences within bird, they did not increase over time showing that shifts in home range, from one 30-day period to the next, caused an increase in cumulative home ranges, even though area-use on a monthly scale did not increase. Since the choice of 30-day home ranges was arbitrary, it would be useful to analyze Mariana Crow spatial behavior at additional temporal scales.

Sub-adult Mariana Crows are socially different from those of other non-cooperatively breeding *Corvus* species. A study of dispersing juvenile Common Ravens (*Corvus corax*) found that individuals made dispersal decisions based on their attraction to conspecifics and anthropogenic food resources (Webb *et al.* 2009). In the relatively less gregarious New Caledonian Crow **(**Corvus moneduloides*)***,** multiple generations of juveniles sometimes accompanied their parents, and unrelated juveniles were often tolerated at feeding tables with family groups (Holzhaider *et al.* 2011). Sub-adult Mariana Crows vocalize infrequently and are most often observed alone (S. Faegre, unpublished data). While juveniles often appear reluctant to move away from their parents (S. Faegre, pers. obs.), they do not appear to be strongly attracted to non-parent conspecifics during the first several months post-dispersal. For example, in this study, two pairs of siblings that were observed together during 75% and 69% of fledgling observations, were observed together during 4% and 0% of post-dispersal (sub-adult) observations. Interestingly, home range overlap of these same sibling pairs only decreased from an average of 79% to 59%, suggesting that changes in behavior, rather than lack of home range overlap, explain the lack of post-dispersal association between siblings.

In common ravens, the aggregation of non-breeding individuals can serve to overcome the defenses of territorial individuals at rich, ephemeral food sources (Heinrich 1988, 2014). In contrast, on Rota, where crows forage primarily on widely occurring insects and small animal prey, it may be less advantageous to compete directly with territorial individuals for food. The low density of conspecific non-breeders and the high potential cost of interactions with territorial pairs may also be factor in the lack of juvenile aggregations among Mariana Crows.

Neighboring Mariana Crow pairs and family groups tended to avoid each other, despite high levels of home range overlap. The home ranges of neighboring family groups overlapped by an average of 46%, while indirect neighbors (which were still close enough to overlap but had a different pair's home range between them) overlapped an average of 37%. During this study, individuals in more densely populated areas had as many as 3-4 direct neighbors and up to two indirect neighbors. Therefore, a given family group would have the chance of interacting socially with up to six additional pairs or family groups during the fledgling period. Despite the high levels of overlap from multiple neighbors, neighboring family groups were rarely observed together. When neighbors did come together, agonistic interactions between adults were common (S. Faegre, pers. obs.).

Home range area curves and analysis of within-individual monthly home range area and overlap revealed dynamic home ranges that did not reach area asymptotes over time. While this was expected for dispersing sub-adults, the lack of stable boundaries in home ranges of fledglings (traveling with their family groups) was surprising and indicates shifts in home range that are atypical among territorial individuals.

Conclusions

Following natal dispersal, daily movements increased by an average of 19% and became more variable, with occasional, large movements of up to 1.6 km in a day. The increased energy expenditure of sub-adults, in addition to their shift to nutritional independence, and the risk of encounters with hostile adults, may increase the risk of mortality during the first several months following natal dispersal. This possibility should be investigated in studies of survivorship.

The dynamic nature of Mariana crow home ranges, with boundaries that shift over time, rather than coalescing into stable areas with defined boundaries, could mean that food resources are patchy and unpredictable, requiring frequent explorations into new areas. However, the same dynamic pattern could result if food resources were plentiful throughout the home range and movements were driven by social factors, such as maintaining distance from neighbors. A study of habitat selection, measuring habitat use in relation to both food resources and neighbor proximity would be useful for better understanding dynamic home ranges in Mariana Crows.

With a better understanding of dynamic home range characteristics of the crow, conservation measures can be designed to best serve them. Currently, the threat of feral cat predation is addressed primarily by trapping in the vicinity of active nests. Due to the high reproductive rate of cats, trapping only in the vicinity of nests is questionable, as it may have no significant impact on the overall population of cats within crow habitat. Additionally, this method may fail to protect family groups, which shift their home range away the nest area shortly after fledglings gain mobility. High first year mortality (Ha *et al.* 2011), much of which occurs between six and 12 months post-fledgling (S. Faegre, unpublished data, Chapter 4), suggests that habitat-wide protection measures will be necessary to address some of the largest threats to species recovery.

Figures

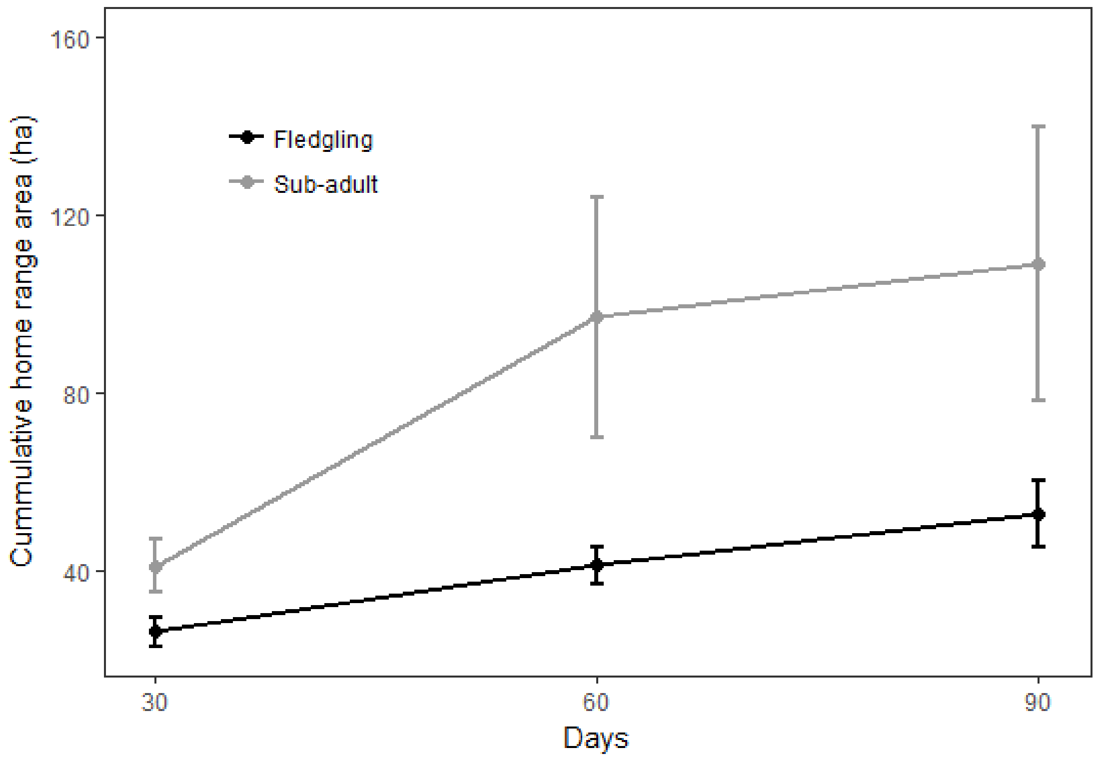

Figure 2.1: Home Range area by age class and days post-fledging or post-dispersal

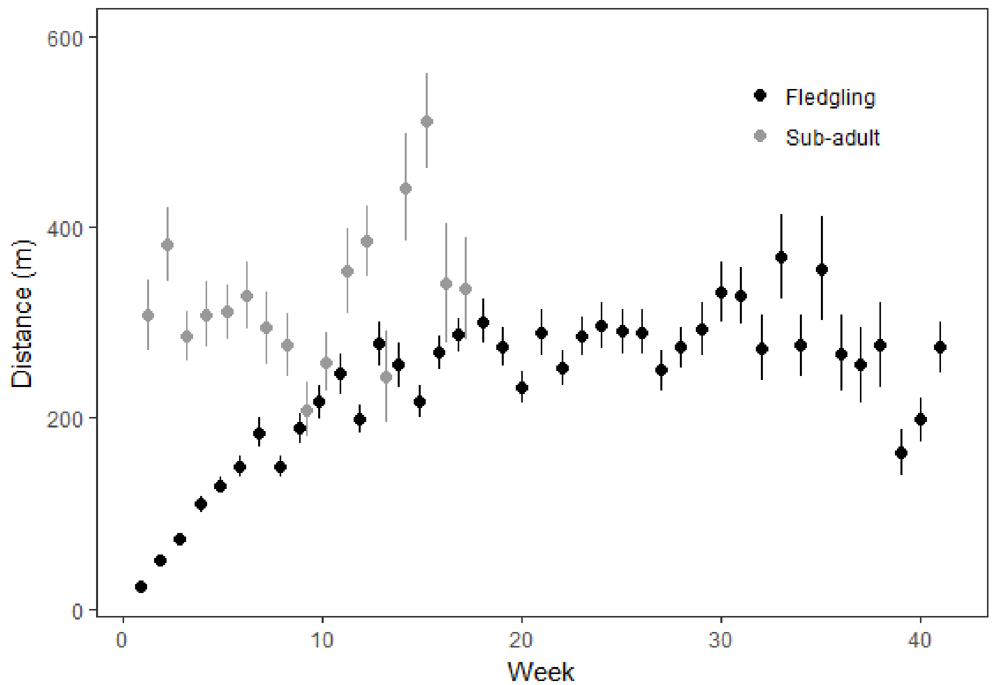

Figure 2.2: Daily movements of fledglings and sub-adults by week post- fledging or dispersal

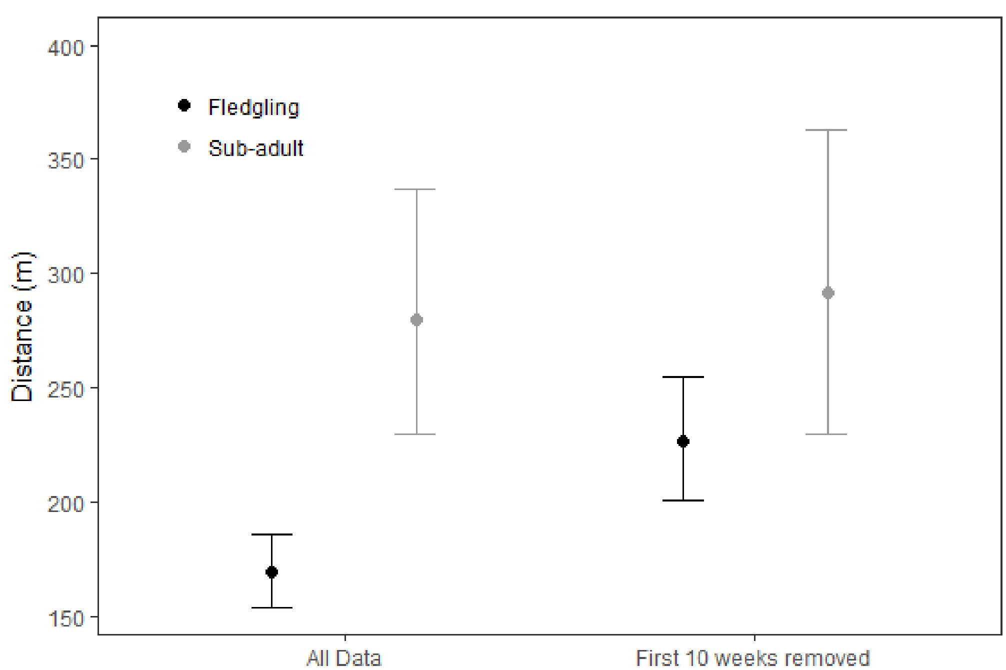

Figure 2.3: Mean daily movement distance of fledglings and sub-adults with and without the first 10 weeks post-fledgling

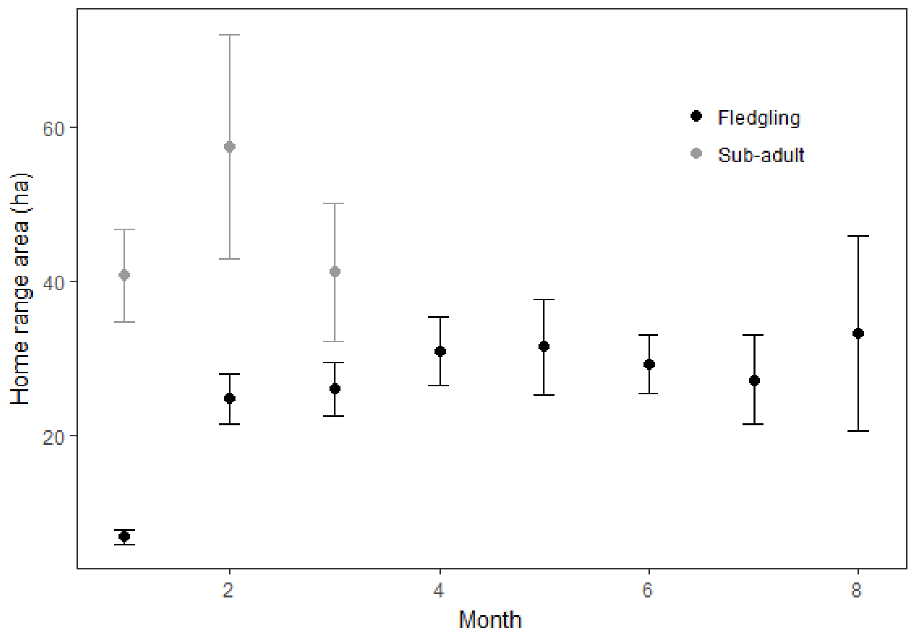

Figure 2.4: Area of sequential 30-day home ranges over month post-fledging or post-dispersal.

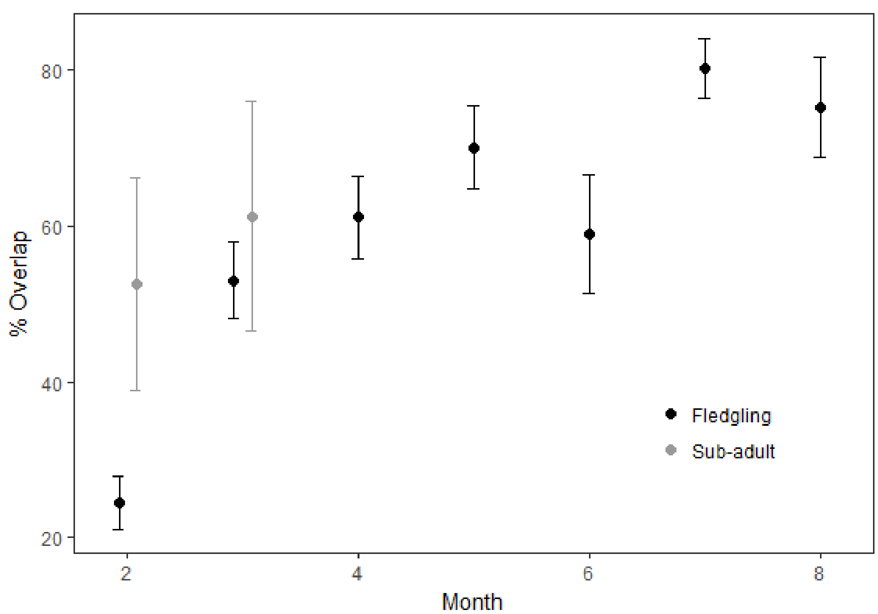

Figure 2.5: Overlap in sequential 30-day home range (within bird) over time post-fledging or post-dispersal.

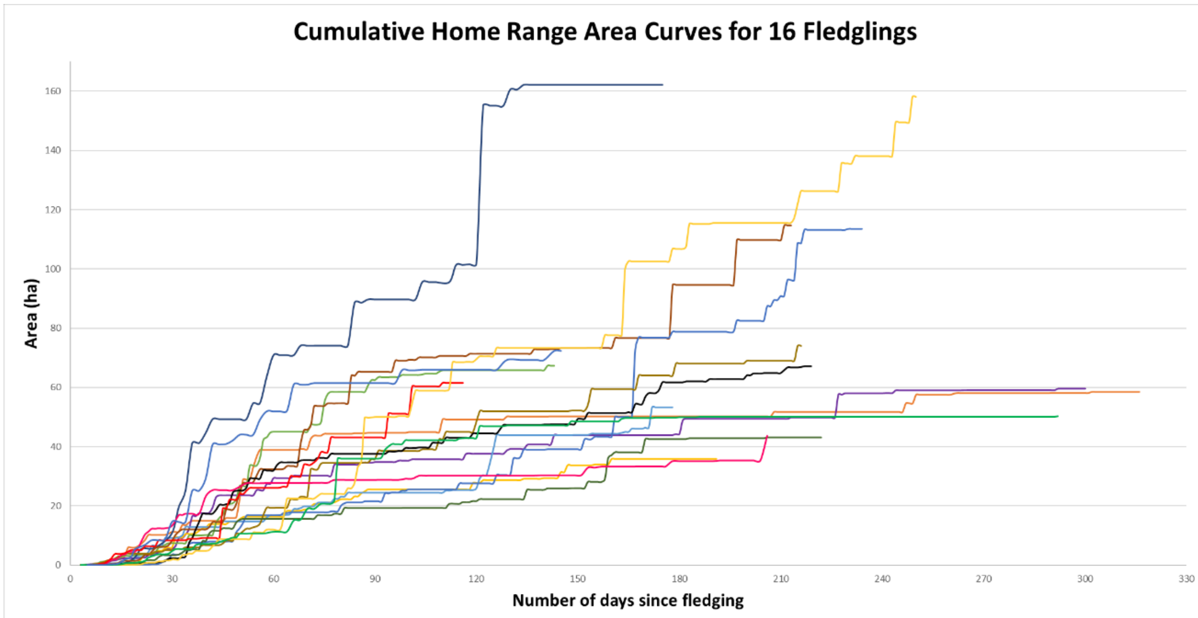

Figure 2.6: Home range area curves for the entire fledgling period

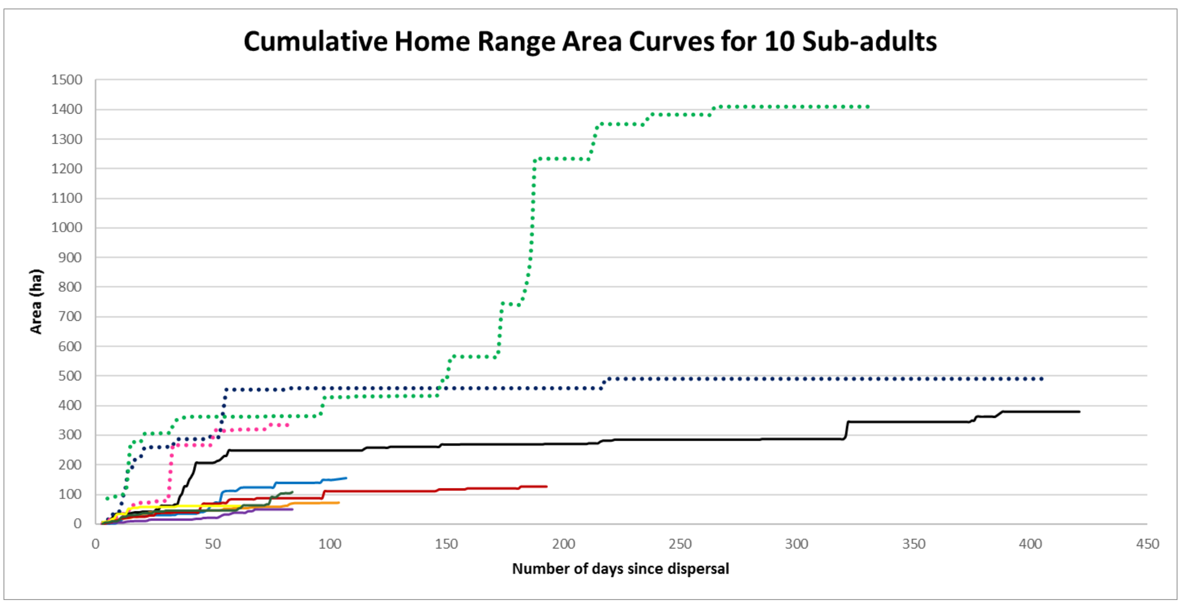

Figure 2.7: Area curves for sub-adults tracked during this study. Dashed lines are individuals that were captured at an unknown age post dispersal (all others begin on day one post- natal dispersal)

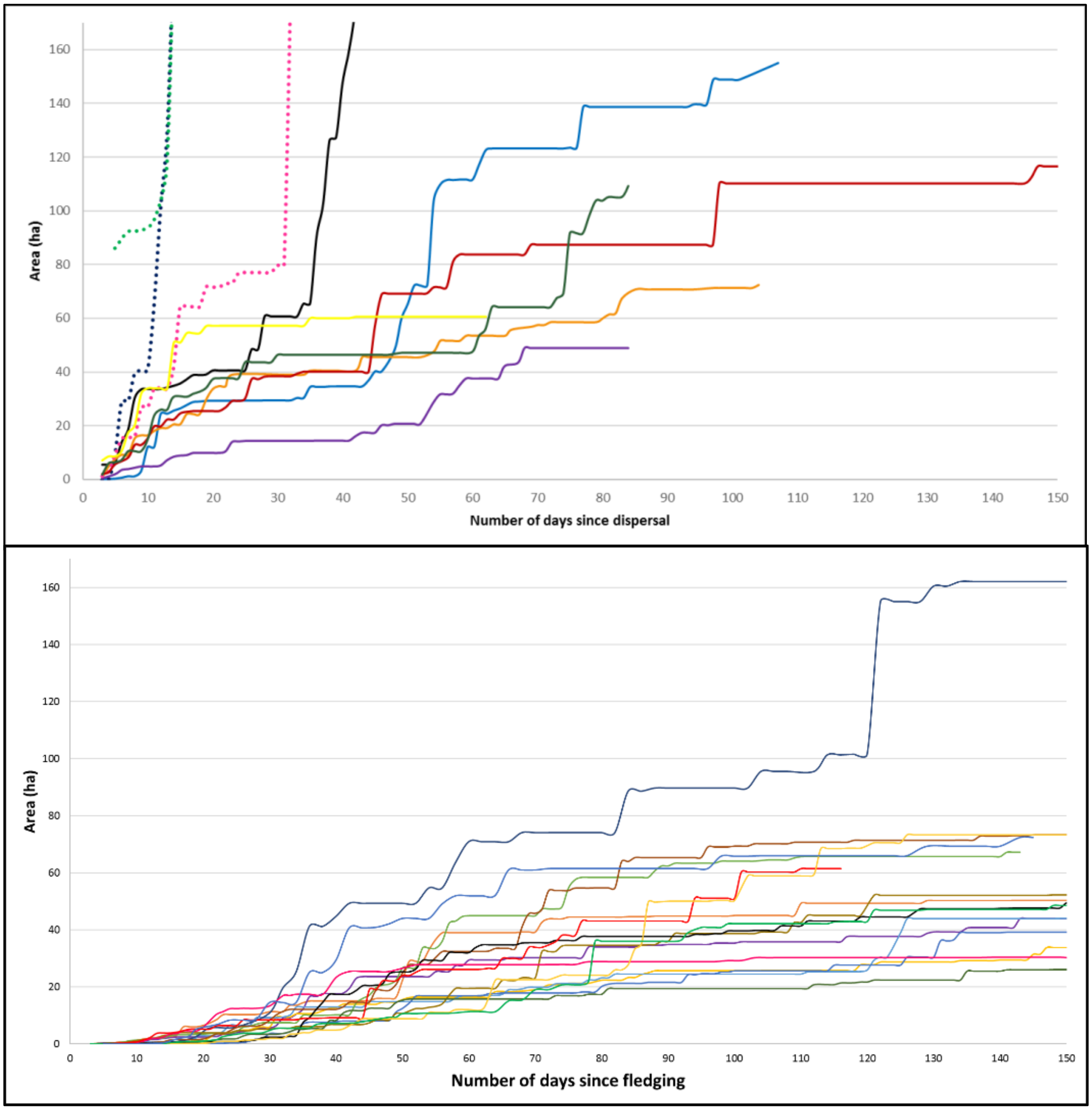

Figure 2.8: area curves during the sub-adult (above) and fledgling (below) periods at equal scales. Dashed lines are individuals that were captured at an unknown age post dispersal (all others begin on day one post- natal dispersal)

Tables

Table 2.1: Home Range area of Mariana Crows

	Mean (ha.)	Range	SD	N
100% MCP Fledgling	76.47	35.83-162.15	38.04	17
100% LoCoH Fledgling	52.65	27.43-115.01	23.35	17
100% MCP Sub-adult	318.7	48.94-1410.01	412.52	10
100% LoCoH Sub-adult	140.62	23.6-558.92	160.73	10

Table 2.2: Percent of home range overlap between Mariana Crow neighbors and siblings

	Mean (%)	Range	SD	N
Adjacent neighbors	45.51	23.21-85.11	20.84	10
Non-adjacent neighbors	37.61	21.6-67.35	17.98	8
Siblings (fledgling)	78.83	54.05-100.0	18.87	4
Siblings (sub-adult)	59.15	45.43-80.8	15.16	4

Chapter 3: Habitat Selection in Mariana Crows

Introduction

Habitats are inherently dynamic, with resources and threats that vary over space and time, generating strong selective pressure for appropriate habitat selection (Cody 1985, Morris 2003). Habitat selection by a species influences survival and reproduction (Brown 1969), and ultimately contributes to population regulation (Newton 1998, Morris 2003). Patterns of habitat use can reveal resources that are critical to animal fitness, and allow inference into the process of habitat selection (Hooten *et al.* 2013). Understanding habitat use and selection are key issues for both ecologists and wildlife managers (Cody 1985, Mayor *et al.* 2009).

Habitat selection is a temporally and spatially scale-sensitive process, making the choice of scale important for habitat selection studies (Mayor *et al.* 2009). The best approach to determining correlation between resource densities and animal location data is a complex issue. Hooten *et al*. (2013) notes that if the resource densities and home range use are developed as separate data sets, then resource utilization functions (RUF) may be created to correlate between the two, allowing for inference into habitat selection. Alternatively, he suggests that in some cases it is better to use a resource selection function (RSF) to understand habitat selection directly from resource data in a use vs. availability framework, in which the utilization distribution is implicit to the analysis.

Habitat loss or degradation is a leading cause of decline in endangered birds worldwide (Johnson 2007) and island ecosystems have suffered a disproportionate number of bird extinctions (Steadman 2006). Information on habitat selection is critical during the designation of protected areas, however this information is often lacking. The Mariana Islands are one such area in which conservation and management efforts would be strengthened by gaining knowledge of habitat selection of the endangered species (USFWS 2005).

The Mariana Islands belong to one of 30 archipelagos within Micronesia and Polynesia that collectively are considered a “biodiversity hotspot” (Myers 2000, Brooks *et al.* 2002). Within this stretch of Pacific Ocean, isolation and restricted range have led to exceptionally high levels of endemism and also to some of the highest extinction rates on the planet (Brooks *et al.* 2002). The Mariana Crow (*Corvus kubaryi*) is a critically endangered forest bird that faces a high risk of extinction (Ha *et al.* 2010, IUCN 2017). The crow is endemic to the islands of Rota and Guam but was extirpated from Guam in the 1990s due to predation by the introduced Brown Tree Snake (*Boiga irregularus*; Savidge 1987). The single remaining population of Mariana Crows is confined to the island of Rota and consists of fewer than 200 individuals (Zarones *et al.* 2015; Kroner & Ha 2017). The Brown Tree Snake is not present on Rota, where the decline has been attributed to habitat loss and degradation, persecution by humans, predation and competition from introduced species, and inbreeding depression (Morton *et al.* 1999, Plentovich *et al.* 2005, USFWS 2005, Wiewel *et al.* 2009, Sussman *et al.* 2015). Little evidence is available to support these hypotheses, although recent evidence from radio-telemetry studies suggests that predation from feral cats (*Felis catus*) may be an important cause of mortality (S. Faegre and R. Ha, unpublished data).

During the 1990s, habitat removal and degradation from human causes and typhoons were linked to the loss of territorial pairs and reduced nest success (Morton *et al.* 1999, Zarones *et al.* 2015). Habitat loss and degradation continue to impact crows to some degree (e.g. disturbance due to the illegal removal of trees, S. Faegre, pers. obs.), but it is unlikely that this is a limiting factor for population recovery, because the percent forest cover is not greatly different now, than it was in 1980 when the population was 1350. Knowledge of Mariana Crow habitat use is essential for the management of remaining Mariana Crow habitat. While certain habitat characteristics have been identified as important in Mariana Crow nest site selection (Morton *et al.* 1999, Ha *et al.* 2011), the nesting area makes up a small percentage of a pair's total home range (Morton *et al.* 1999, S.F. unpublished data) and habitat selection outside of the nest area has never been studied.

Habitat selection is defined as the disproportional use of a habitat relative to its availability (Jones 2001). Within an individual's home range, selection can be inferred by evaluating habitat differences in areas of the home range that have disproportionally high and low levels of use. Most animals use space heterogeneously and have areas of high-intensity use, or core areas, within their home range, where movements are restricted to a smaller area than expected, based on levels of mobility (Börger *et al.* 2008, Van Moorter *et al.* 2009). Core areas may have stable habitat characteristics that make them particularly attractive to individuals in the long term, or they may shift over time as resource abundance and social opportunities change (Benhamou & Lambert 2012).

Despite the dynamic, shifting nature of Mariana Crow home ranges (S. Faegre, unpublished data, Chapter 2), family groups have small, intensively used core areas, to which they return irregularly during the 8-month average fledgling period. Food needs are high for parents with dependent offspring, and predation risks are particularly high for juveniles in the post-fledging period (Cox 2014, Naef-Daenzer & Grüebler 2016). Because of these selection pressures, we expected food resources, predators, and the vegetation characteristics supporting them, to be the most important variables driving patterns of habitat use within the home ranges of Mariana Crow family groups.

While resource utilization functions are the preferred method of analyzing habitat use within the home range, the necessity of a background layer of important environmental measurements was problematic at our study site, where land-use and habitat types have not been delineated in enough detail to reflect the selection process of our study species. Additionally, we were unable to measure prey variables on a large enough scale to create a gradient over each animal's utilization distribution. Due to these constraints, we confined habitat measurements to core and outer areas of each home range, to try to capture the potential extremes, rather than a gradient of values throughout the entire utilization distribution.

Based on the predictions of optimal foraging theory, we hypothesized that the frequency of use by family groups would be explained, in part, by variations in food resource density and vegetation characteristics supporting key prey species. We estimated the relative abundance of three common prey taxa: geckos, *Coenobita* hermit crabs, and *Vespidea* paper wasp larvae (S. Faegre unpublished data, Chapter 1), and predicted that core areas would have higher densities of these items than outer areas. We also estimated abundance of coconut crabs (*Birgus latro*), rats (*Rattus sp*.), feral cats (*Felis catus*), and junglefowl (*Gallus gallus*), and hypothesized that activity of predators (cats) and potential competitors (rats and junglefowl) would be lower in core areas than outer areas. Since vegetation characteristics may co-vary with animal variables, we hypothesized that vegetation characteristics would also vary between core and outer areas; however, we did not have specific predictions about the direction of these relationships.

Methods

Study area

Rota is the second most southerly island after Guam in the Mariana Islands, Western Micronesia (14°09'N, 145°12'E). The 85-km^2 island is volcanic in origin with uplifted limestone terraces. The climate is tropical, with high humidity. Wet and dry seasons are typically from July-November (wet) and January-May (dry) with rainfall measuring from a minimum of 3.69 mm/month in March to a maximum of 13.37 inches/month in September (Lander & Guard 2003). Rota is located within the Western Pacific typhoon belt and experiences typhoons periodically but no typhoons occurred during this study.

Radio-tracking

Between March 2010 and February 2013, 11 Mariana Crows were radio-tagged within several days of fledging and tracked using Holohil RI-2CT VHF transmitters. Transmitter/harness packages were 3-4% of the body weight of each crow and were fitted to individuals using a backpack design with a weak link system incorporated. This study included home ranges of tagged fledglings and their family groups. The fledgling period was defined as the period of nutritional dependence on their parents, prior to natal dispersal. During daily or bi-weekly observations, tagged crows were observed and social interactions and other behaviors were recorded to determine dispersal status.

Crows were tracked until death or until failure of the radio-tag, and only individuals that survived for at least six months post-fledging were included in this study. A cut-off of six months was chosen based on the deaths of several birds shortly after six months and because a six-month period was considered adequate to define high and low use areas within the family group's home range. When siblings were radio-tagged, only one sibling from the pair was used in the study to avoid pseudoreplication.

Plot selection

We chose the fixed K local convex hull method (LoCoH; Getz & Wilmers 2004) to characterize home ranges because this method represents space use more accurately within landscapes characterized by sharp topographical features and fragmented habitats (Getz & Wilmers 2004, Getz *et al.* 2007). Furthermore, unlike kernel-based methods, the fixed K LoCoH is robust to changes in the smoothing parameter (Getz *et al.* 2007), reducing the potential for biased results and improving the accuracy of inter-individual comparisons.

During June 2013-January 2014 we sampled vegetation characteristics and predator and prey abundance in frequently used "core" areas and infrequently used "outer" areas of crow home ranges (Figure 1). After exploring the differential exclusion of habitat from home ranges by varying the outer boundaries between 100% and 95%, we chose the 98% isopleth as the most representative of total home ranges for the family groups in this study. We defined the outer 10% of the home range (between the 88% and 98% isopleths) as the outer area, and the inner 50% isopleth as the core area. The area between the 50% and 88% isopleths was not sampled. The first 31 days post-fledge were removed from this analysis because this is a period when fledglings are severely restricted in their habitat use due to limited mobility (S. Faegre, unpublished data, Chapter 2).

Due to limitations in the number of plots we could sample, we employed a use-only design, restricting our sampling locations to points in which individuals were actually observed during radio-tracking. This ensured that plots were located in habitat used by that individual, increasing our ability to distinguish between variations in food density at locations where crows had been observed.

We randomly selected six points from telemetry locations with three in the core and three in the outer areas of each home range. These formed center points for 289 square-meter circular plots (9.6 m radii). Center points were adjusted by up to 10 meters, as needed, to avoid including large cliffs or areas of non-habitat (e.g. fields, roads, etc.). Sheer, non-traversable cliffs were avoided for practical reasons, and areas without woody vegetation were considered non-habitat and were thus excluded from plots. To increase the probability of representing diverse habitats, points were separated by a minimum of 50 meters in core areas and 150 meters in outer areas. These distances were chosen by exploring the maximum spread of points that did not result in forced placement of plots along edges of the smaller core and outer areas.

Resource Measurements

Within each plot, we counted and identified all woody stems (live or dead) reaching breast height. The height of each stem (understory, canopy, or super canopy) was noted and stems greater than 10 cm diameter at breast height (DBH) were measured. We estimated canopy and super canopy heights using a rangefinder.

We counted common animal species, including prey items (geckos, paper wasp larvae, and hermit crabs), predators (feral cats), and other animals that were common and had uncertain relationships to Mariana Crows (rats, coconut crabs, and junglefowl). We measured paper wasp larvae abundance by counting the number of paper wasp nests within each plot.

Geckos surveys were completed from June-November 2013, using visual searches which were conducted in pairs, consisting of one core and one outer area plot from a single home range that were surveyed sequentially on the same night. Visual gecko surveys were carried out using methods similar to Wiles et. al (1990). Between 19:30 and 23:30 an observer walked slowly through the study plot, using a high-powered headlamp to scan for geckos in trees and on the ground. In addition to the visual search, the observer used a 2-meter long stick to agitate vegetation, allowing the detection of hidden geckos that fled from hiding places due to mechanical disturbance. The duration of gecko surveys was 40 minutes per plot. Geckos were captured by hand whenever possible; after capture each animal was identified, weighed and released. Geckos that were observed but not captured were identified when possible and their weight was estimated. Gecko abundance measures included counts and total grams of geckos per plot. Gecko species assemblages were measured by number of species per plot, as well as number of individuals of each of the six species that occurred within plots.

Between December 2013 and August 2014, we surveyed hermit crabs, coconut crabs, rats, cats, and junglefowl in plots, using trail cameras to record animal activity at bait boxes over a 5-day period. Bait boxes were filled with large chunks of mature coconut, with the inner husk attached. Additionally, a can of tuna was dumped in front of each bait box as an additional attractant. The bait boxes measured 8x5x5 inches and were made of two layers of 1/2x1 inch hardware cloth. The mesh size was chosen with the intention of excluding Coconut Crabs from accessing the bait, while allowing hermit crabs to reach it. However, large Coconut Crabs were able to bend the wire mesh and access small amounts of bait. Each bait box sat on top of a black, rectangular piece of tarp, measuring 35x21 inches. The bait box was arranged on the tarp such that a 10X21 inch portion of the tarp lay flat on the ground in front of the bait box, a 14x21 inch portion rose vertically behind the box, and six inches of tarp remained on either side of the bait box (Figure 2). Trail cameras were attached to a tree, approximately two meters from the bait box. All plots within a given home range were sampled simultaneously.

Due to the slow movements of hermit crabs, they often failed to trigger the trail cameras' motion-sensors, therefore trail cameras were set to time lapse, taking photos every 10 minutes, in addition to motion-detection settings, which allowed for the detection of other animals that approached the bait box (e.g. cats, rats and birds). While time lapse photos were useful for measuring the activity of animals that were present much of the time (such as hermit crabs, rats and Coconut Crabs), they did not collect representative data on other species.

Trail camera photos were coded in different ways depending on the animal species. For hermit crabs, Coconut Crabs and rats, we only coded photos taken at 10-minute time lapse intervals during the first 24 hours that the camera was in place, and only animals touching the tarp were counted. However, after finding that Coconut Crabs often excluded rats from the tarp, we added a variable in which we counted any rat in the photo. Cats and junglefowl appeared less frequently and rarely touched the tarp; therefore, we counted all occurrences of cat and junglefowl activity over the 5-day period (including both time lapse photos, and photos triggered by the motion sensor).

In addition to resource measurements, we measured the distance of each plot to the nearest road.

Statistical Analyses

We conducted a 2-stage analysis of results: 1) Principal Components Analysis (PCA) was used to reduce a large number of variables into independent factors, with separate PCAs for prey and vegetation variables, and 2) and Discriminant Function Analysis (DFA) was used to identify which variables most accurately identified plots as either core versus outer areas of home ranges.

Species (animal or vegetation) that were counted in less than half the plots were eliminated from the analysis. All statistical analyses were conducted in SYSTAT v10 (Wilkinson 19xx).

We used the Shapiro–Wilk test to check for normality of animal counts and vegetation characteristics and transformed variables using log-n, log-10 or square root transformations where necessary to achieve normal distributions. As some of the 14 animal, and 34 vegetation variables were likely to be correlated, we performed two PCAs to generate two sets of uncorrelated variables. We then used a scree plot to select animal and vegetation characteristics that accounted for the most variance and used the resulting five animal factors and 10 vegetation factors in a DFA to test which factors best predicted whether a plot was in a core or outer area. Jack-knifed classification percentages were reported in all cases.

Results

All animal taxa surveyed, except junglefowl, were found in the home ranges of each of the 11 family groups in this study. We identified six gecko species, including *Lepidodactylus lugubrus, Gehyra mutilata, Nactus pelagicus, Perochirus ateles, Gehyra oceanica, and Hemidactylus frenatus.* However, only *G. oceanica* and *G. Mutilata* occurred frequently enough (more than half the plots) to be included in the analysis at the species level, while the others were included in the measures of total gecko numbers, mass, and species diversity. *Coenobita* hermit crabs and *Vespidae* paper wasps were not identified to species.

Principal components analysis yielded 10 independent vegetation factors and five prey factors (Tables 1 & 2), explaining 74.05% and 80.61% of the total variance in vegetation and prey respectively. There was high variability in many of the habitat factors measured. For example, among plots, hermit crab counts ranged from 0 to 23 and gecko mass ranged from 0 to

190 grams. However, the results of the DFA suggested that none of the prey or vegetation factors were predictive of core and outer areas (Jackknifed Classification, Wilks Lambda=0.6739, *df* = 15, 1, 59, approximate $F = 1.459$, $p = 0.163$).

Discussion

We were unable to identify any distinguishing characteristics of core versus outer areas of Mariana Crow home ranges. Four hypotheses that may explain this result include: 1) Mariana Crows are not food or habitat-limited and other factors (social factors, memory/familiarity with place) are primary drivers in habitat selection within the home range, 2) Differences in core and outer areas occur at the landscape level and could not be detected within this use-only design, 3) important prey, predator, or vegetation characteristics, remained unmeasured, and 4) important animal variables were ephemeral and measurements taken at a later date were not representative of characteristics during the time crows were using the area. Memory, and familiarity with place, are key in the spatial behavior and habitat selection of many species (Van Moorter *et al.* 2009, Wolf *et al.* 2009, Piper 2011, van Overveld *et al.* 2011, Van Moorter *et al.* 2013), and are likely to be important factors for long-lived species with high site fidelity, such as the Mariana Crow.

The lack of consistent vegetation and prey differences in core and outer areas in this study may be an accurate representation of habitat within this use-only design, suggesting that adequate prey and forest characteristics are present throughout used portions of the home range. Our findings within plots can be generalized to the portions of core and outer areas that are used by crows, but not to the entirety of areas bounded by core or outer area polygons. One limitation of the use-only sampling method is that we were unable to determine if the amount and distribution of non-habitat or unused habitat within core and outer areas influenced differential use of the larger core and outer areas by the birds. Given that we did not find differences between used portions of habitat in core and outer areas, an investigation of larger-scale differences is warranted.

Mariana crows may evaluate different sets of variables when selecting habitat in areas that are occupied by conspecifics, as compared to vacant habitat. Given the high percentage of overlap between neighboring home ranges, and the agonistic interactions that tend to occur when neighbors coincide at the same location (S. Faegre, unpublished data, Chapter 2), it is likely that spacing of conspecifics is a strong driver of habitat selection within the home range. In this study, only one family group's home range included outer areas that were free of neighboring conspecifics. Due to neighbor overlap, the core areas of family groups were often suspected (and in one case, confirmed; Figure 1) to be outer areas of one or more other neighboring family groups, which may have confounded the distinction between core and outer areas in this study.

Habitat selection is often density dependent (Mobæk *et al.* 2009, Beest *et al.* 2015) and, while the low population density of crows on Rota makes density-dependent processes less likely, a future study of Mariana Crows could be designed to include the effects of conspecific density and proximity. For example, habitat selection could be measured in low-density areas, where crows do not have direct neighbors or, alternatively, a study in high-density crow habitat could involve quantification conspecifics.

Even seldom used portions of the home range can be critical. In this study, for example, one pair's nesting area fell outside of their 98% home range during the 7-month period of fledgling dependency (Figure 1). Overall, the lack of distinguishing habitat characteristics in core versus outer areas suggests that all portions of Mariana Crow home ranges have important resources and that future study is needed to better understand Mariana crow habitat selection.

Figures

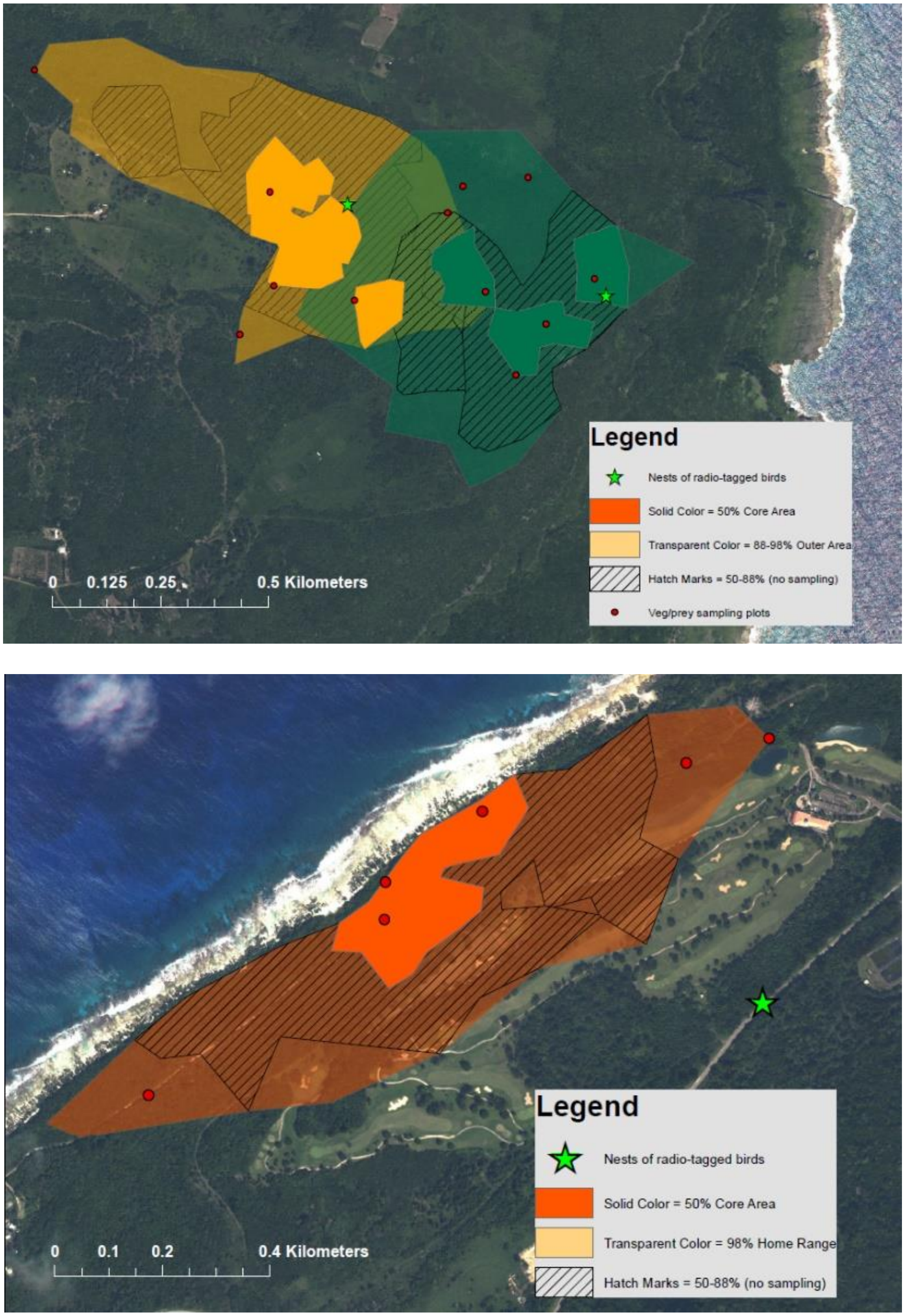

Figure 3.1: Pre-dispersal home ranges of Mariana Crow fledglings (above: neighboring family groups; below: family group whose nest is outside of their 98% home range)

Figure 3.2: Bait boxes at two plots

Tables

Table 3.1: Vegetation and Landscape Components

	Factor loading	Variance explained by rotated component	% of variance explained
Pandanus sp. (count and DBH)	-0.93	4.55	13.38
Potential nest trees (count)	0.79	2.56	7.54
Understory characteristics (density, species)	0.87	3.33	9.79
Ficus sp. (count, DBH)	-0.90	2.38	7.01
Canopy characteristics (height, species)	0.82	2.40	7.07
Distance to road	0.78	2.33	6.84
Neisosperma oppositifolia (count, DBH)	-0.73	2.12	6.23
Square area dead stems	0.84	2.06	6.07
Psychotria mariana (count)	-0.76	1.96	5.77
Tree species	0.87	1.48	4.35
Total			74.05

Table 3.2: Animal Components

	Factor loading	Variance explained by Rotated component	% of variance explained
Geckos (*G. Oceanica*, count, mass)	0.95	2.48	17.72
Rats	0.96	2.60	18.59
Hermit crabs	0.98	2.66	16.12
Cats	0.87	2.134	15.19
Gecko species (*G. Mutilata*, total)	-0.88	1.82	12.99
Total			80.61

Chapter 4: Correlates of First Year Survival in Mariana Crows

Introduction

Differential juvenile survival explains a large part of the variance in lifetime reproductive success, yet the processes driving variation in survival are poorly understood (Cox 2014). Among altricial birds, the post-fledging period is a particularly critical time, during which body condition and behavior of fledglings are strong predictors of mortality (Naef-Daenzer & Grüebler 2016). The age and level of physical development at fledging vary greatly between species but little within species (Roff *et al.* 2005, Martin 2015), suggesting that these characteristics have evolved in response to species-specific pressures in most birds. Within species, mass and wing length correlate positively with survival during the early fledgling period (Cox 2014, Naef-Daenzer & Grüebler 2016). These traits are closely related to energy intake, which relates directly to resource availability. While habitat characteristics, such as food availability, are the most commonly cited factors affecting nestling and fledgling condition (Cody 1985, Cox 2014, Naef-Daenzer & Grüebler 2016), other characteristics, such as genetic heterozygosity, parent quality, hatching order, sex, and some types of disease, can be largely independent of habitat factors, and can also have direct effects on fledgling condition, behavior, and survival (Maness & Anderson 2013, Cain *et al.* 2014, Zárybnická *et al.* 2015).

In addition to its direct effect on fledgling body condition, resource distribution and predictability are important drivers of both spatial and social behavior (Barraquand & Murrell 2012, Macdonald & Johnson 2015). Energy limitation, such as lack of sufficient resources in the home range, can affect spatial behavior by driving birds to travel longer distances to find food, or by preventing them from making the necessary movements due to poor physical condition (Naef-Daenzer & Grüebler 2008, Rechetelo *et al*. 2016). The feedback loop between energy limitations and spatial behavior can perpetuate the differential in fledgling body condition over time. Spatial behavior, including home range size and daily movements, have been proposed as one proximate mechanism which can mediate the effect of fledgling condition on later survival (Naef-Daenzer & Grüebler 2008), however this relationship has rarely been studied.

Most studies of post-fledging survival in altricial birds account only for the first 4-8 weeks post-fledging, and the highest mortality rates are usually found during the first three weeks (Maness & Anderson 2013, Cox *et al.* 2014). Predation is a common cause of post-fledging mortality, and measures of physical development and fitness (wing and mass) can have direct consequences in predator avoidance (Haché *et al.* 2014, Naef-Daenzer & Grüebler 2016). Few previous studies have examined the relationships between fledgling characteristics and survival in a sample of birds that survived beyond the first eight weeks post-fledging, and some authors have hypothesized that fledgling characteristics are less likely to impact survival beyond the early post-fledging period (Maness & Anderson 2013).

The Mariana Crow (*Corvus kubaryi*) is a critically endangered forest bird that faces a high risk of extinction (Ha *et al.* 2010, IUCN 2017), in part due to low first year survival (Ha *et al.* 2011). The crow is endemic to the islands of Rota and Guam but was extirpated from Guam in the 1990s due to predation by the introduced Brown Tree Snake (*Boiga irregularus*; Savidge 1987). The single remaining population of Mariana Crows is confined to the island of Rota and consists of fewer than 200 individuals (Zarones *et al.* 2012, Kroner & Ha 2017). The decline on Rota has been attributed to habitat loss and degradation, persecution by humans, predation and competition from introduced species, and inbreeding depression (Morton *et al.* 1999, Plentovich *et al.* 2005, USFWS 2005, Wiewel *et al.* 2009, Sussman *et al.* 2015).

We studied the relationship between body measurements at fledging, spatial behavior, and first year survival in radio-tagged Mariana Crows. Like other passerines, Mariana Crows have high mortality rates during the first several weeks post-fledging; however, the species has a long period of post-fledging parental care (eight months average, Morton *et al.* 1999) and re-sighting data from color banded birds suggests that mortality may remain high throughout the fledgling period (R. Ha, unpublished data). In a sub-set of individuals that survived a minimum of four months post-fledging (the time period needed to collect sufficient home range data), we studied the relationships between spatial behavior, fledgling characteristics and survival. We tested the hypotheses that, 1) mass and wing at fledging would be smaller in birds that died, 2) the relationship between physical measurements and survival would persist, but with less strength, in the sub-set of individuals that survived at least 4 months post-fledging, and 3) that post-fledging home range size and daily movements would correlate positively with physical measurements and be larger in birds that survived their first year.

Methods

Study system

Rota is the second most southerly island after Guam in the Mariana Islands, Western Micronesia (14°09'N, 145°12'E). The 85-km^2 island is volcanic in origin with uplifted limestone terraces. The climate is tropical, with high humidity. Wet and dry seasons are typically from July-November (wet) and January-May (dry) with rainfall measuring from a minimum of 3.69 inches/month in March to a maximum of 13.37 inches/month in September (Lander & Guard

2003). Rota is located within the Western Pacific typhoon belt and experiences typhoons periodically.

Radio-tracking

From 2009-2016, we radio-tagged 24 fledgling Mariana Crows with Holohil RI-2CT VHF transmitters, which had an average battery lifetime of 12 months. Transmitters with harnesses were 3-4% of the body weight of each crow and were attached using a backpack design with a weak link system incorporated. Crows were tracked until death or failure of the transmitter. Twenty-two of these fledglings (from 18 family groups) were tracked until death or throughout their first year post-fledging. Twenty birds had measurements taken within 4 days of fledging; only these individuals were used in analyses of physical characteristics. Two fledglings were tracked throughout their predispersal periods, for five and seven months post-fledging, but their survival after dispersal was unknown so they were included in correlation analyses but not mortality analyses. When siblings were radio-tagged, both were used in the analyses of physical characteristics and survival but, to avoid pseudoreplication, only one sibling from each pair was used in the analyses involving post-fledging home range or daily movements.

Crows were classified as fledglings during the period of nutritional dependence on their parents, and as sub-adults after reaching independence from their parents but prior to their first nesting attempt. Nutritional independence from the parents almost always coincides with dispersal from the natal territory, which occurs at an average age of eight months post-fledging (Morton *et al.* 1999, S. Faegre, unpublished data). During daily or bi-weekly observations, tagged crows were observed from a distance of 2-10 meters. Social interactions and other behaviors were recorded to determine dispersal status.

Banding and Measurements

Fledgling Mariana Crows were captured by hand and banded with an aluminium USFWS band and up to three plastic color bands. Measurements, including mass, wing cord (unflattened), tail length, tarsus length, and two bill measurements were also taken (Pyle 1987).

Data Analysis

To determine whether mass or wing length at fledging was associated with first year survival, we used two independent t-tests with survival (dead vs. alive at 1 year post-fledge) as the grouping variable and either mass or wing length as the test variable. We also conducted t-tests for the sub-set of individuals that survived 4+ months post-fledging. We did not employ a correction factor to p-values, due to the risk of inflating an already-increased risk of making a type II error due to low sample size (Nakagawa 2004).

We used three linear mixed effects models to explore the effects of time post-fledging (30, 60, 90, and 120 days) and first year survival (dead vs. alive) on three dependent variables: Home range size, core area size, and daily movement distance. Bird ID was used as a random effect for all models. Home range measures were square-root transformed and distance measures were cube-root transformed to satisfy the assumption of homogeneity of variance.

We computed Pearson product-moment correlation coefficients to assess the relationships between 1) home range and wing, 2) home range and mass, 3) mass and wing, 4) daily movements and wing, 5) daily movements and mass, and 6) daily movements and home range. While these data came from a total of 24 birds, each type of measurement (body size, home range, and daily movements) was available for a smaller sub-set of the total. Therefore, the correlations were done separately from one another to maximize the sample size in each. For these analyses, home ranges and daily movements were calculated from the first 30 days post-fledgling.

Analyses were done using IBM SPSS Statistics 19 and package *nlme* in R (Pinheiro et al. 2017).

Results

Twelve of 22 crows died during their first year post-fledging (Table 1). Only one bird died during the first three weeks post-fledging, while four died between months one and four, and six died between months six and 12. Eight of the 10 crows that survived their first year were recruited into the breeding population by 2017.

Birds that survived had longer wings (M = 192.11 mm, SD = 6.85) than those that died (M = 179.18 mm, SD = 10.57, t (18) = 3.159, p = 0.005), but there was no significant effect of mass on survival (t (18) = 1.23, p = 0.233). For the sub-sample of birds that survived at least four months post-fledging, the effect of wing length on survival remained (t (13) = 4.219, p = 0.001) while the effect of mass remained non-significant.

Birds that survived had larger home ranges (M = 31.96 ha, SE = 3.52) than those that died (M = 22.21 ha, SE = 3.52, F (1, 13) = 4.219, p = 0.001). Home range size also increased with days post-fledge (F (3, 28) = 86.10, p < 0.0001). Core area size (50% isopleth) increased with days post-fledge (F (3,38) = 40.15, p < 0.0001, Figure 2), but there was not a significant effect of survival (F (1,13) = 2.86, p = 0.11).

A visual examination of home range area curves (cumulative home range) for fledglings during their entire pre-dispersal period suggested that the difference in home range area, for birds that died vs. survived, was greatest during the first several months post-fledgling and declined as the birds aged (Figure 3). In two cases, the home range areas of fledglings that later died increased dramatically around 160 days post-fledging due to loss of one parent, and the continued persistence of the fledgling in following the remaining parent, as the parent ranged into new areas, presumably in search of a new mate.

Birds that survived had longer daily movements (M = 204.85 ha, SE = 6.51) than those that died (M = 154.91 ha, SE = 5.96 (F (1, 6) = 24.515, p = 0.003, Figure 4), and individuals increased their daily movement distance with age post-fledge (F (3, 30) = 59.67, $p < 0.001$). Additionally, there were correlations between wing and daily movements (r = 0.652, n = 13, p = 0.016), wing and home range (r = 0.513, n = 15, p = 0.05), wing and mass (r = 0.577, n = 19, p = 0.01), and home range and daily movements (r = 0.565, n = 15, p = 0.028, Table 2). There was no significant correlation between mass and home range (r = 0.227, n = 15, p = 0.416), or mass and daily distance (r = 0.115, n = 13, p = 0.709).

Discussion

Fifty-five percent of fledglings in this study died during their first year post-fledging and half of these deaths occurred between months six and 12, just before or after natal dispersal. Among 20 birds that were measured within four days of fledging, wing cords varied from 166-200 mm. All six individuals with wing cords of less than 180 mm died during their first year post-fledging. Of the 14 individuals with wing cords greater than 180 mm, 71% survived.

The majority of deaths were ruled cat predations, based on the appearance and locations of the remains. Reduced wing length and spatial movements in birds that died suggests that either delayed development or early fledging affected spatial behavior and led to increased susceptibility to predation. However, since none of the crows in this study were depredated until long after flight feather growth was finished, reduced fledgling wing length and spatial behaviors may also be indicators of underlying issues (e.g. inbreeding, illness, habitat quality, parent quality) that cause long-term susceptibility to predation.

Unlike most passerine species, the stage of development at fledging varies greatly among individual Mariana Crows, with wing cords ranging from 145-203 mm, when measured within four days of fledging (R. Ha unpublished data). Since predation pressure is one of the main forces shaping the evolution of species-specific fledgling characteristics (Roff *et al.* 2005, Martin 2015), the Mariana Crow's evolutionary history, on islands without native predators, may explain its intraspecific variability at the fledgling stage. Large nestlings often hopped in and out of their nest during the days prior to fledging, and most fledglings were first found within several meters from their nest (S. Faegre, pers. obs.), suggesting that force-fledging (by predators or other disturbance) is unlikely to be a cause for this variability in development of fledgling Mariana Crows.

Few studies have examined the relationship between animal fitness (measured by survivorship or by phenotypic or genotypic variations) and home range size. Cain *et al.* (2014) found that multi-locus heterozygosity correlated positively with home range size in the critically endangered Black Rhinoceros (*Diceros bicornis*), while Beckman and Lill (2016) found a correlation between number of teats (a proxy for reproductive potential) and home range size in female agile antechinuses (*Antechinus agilis*). Naef-Daenzer and Grüebler (2008) found that home ranges of Great Tit (*Parus major*) fledglings with larger mass were nearly twice the size of those with low mass, and that frequency and speed of movements within the home range were similarly affected by body condition. The results of the current study show that Mariana Crow home ranges were 33% smaller, and daily movements were 31% shorter, for family groups of fledglings that died, compared to those that survived their first year. Daily movements and home range area were positively correlated with wing length, suggesting that decreased spatial behavior during the first 30 days post-fledging was due to decreased flight ability.

During daily behavioral observations, radio-tagged fledglings were accompanied by an average of 1.66 parents (S. Faegre, unpublished data), suggesting that family units spend most of their time together and move through their home ranges as a group. A fledgling's inability or unwillingness to follow a parent may impact parent movement decisions and home range of the family group, especially early in the fledgling period when fledglings rely entirely on parental feedings.

Home range area curves for fledglings (Figure 3) shed some light on this issue. While the home range area during the first 120 days post-fledging is dramatically smaller in birds that died, home range areas become more similar after 120 days. Daily movements showed a similar pattern, with differences between groups leveling out after 90 days post-fledging (Figure 4). This decrease in difference over time may be due to the accumulation of other factors that impact parent movement decisions, such as the loss of a parent, or a change in the parent-fledgling relationship. For example, parents may reduce their attendance to older fledglings that fail to follow them in their normal movements (S. Faegre, pers. obs.).

The earliest dispersal in our study occurred at 120 days post-fledging, indicating that some fledglings have the ability to be nutritionally independent of adults at this age. After 120 days, parents may become more attuned to their own needs than those of their fledglings, which could cause home ranges of fledglings to shift and enlarge if they continue to follow their parents beyond this point.

Conclusions

Future work should aim to uncover the mechanisms behind this study's findings of an enduring relationship between fledgling characteristics and first year survival. To test the resource limitation hypothesis, data could be collected on resource availability and quality of parental care in pairs with nestlings, to look for correlations between resources, parental care, and fledgling physical and behavioral characteristics. To test the "poor quality fledglings hypothesis", a study could collect data on wing cord, home range, and survivorship for sequential sets of offspring from known pairs, to determine if fledgling home ranges and measurements vary with survivorship when area/territory and parent identity are controlled for. Additionally, it would be valuable to compare inbreeding coefficients of individuals that died versus survived their first year post-fledging. If future studies support the resource limitation hypothesis, we recommend supplemental feeding during the nestling and early fledgling period to improve fledgling outcomes.

Figures

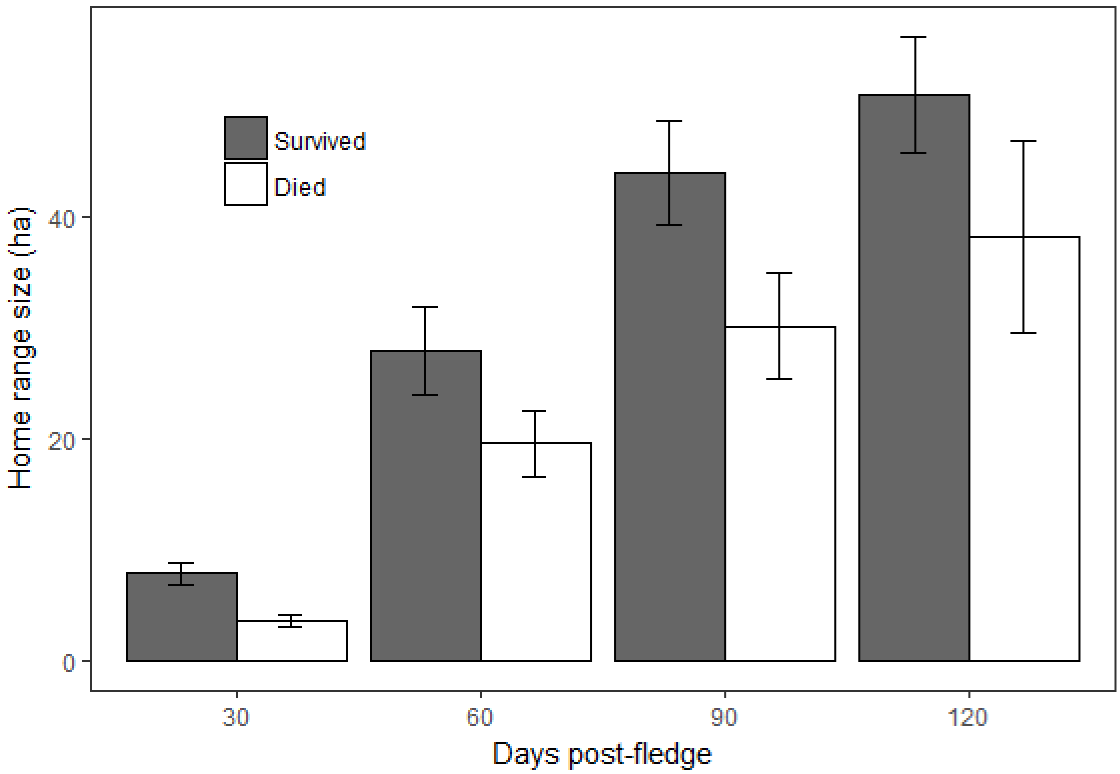

Figure 4.1: 100% home range area (cumulative) in birds that survived versus died during their first year post-fledging

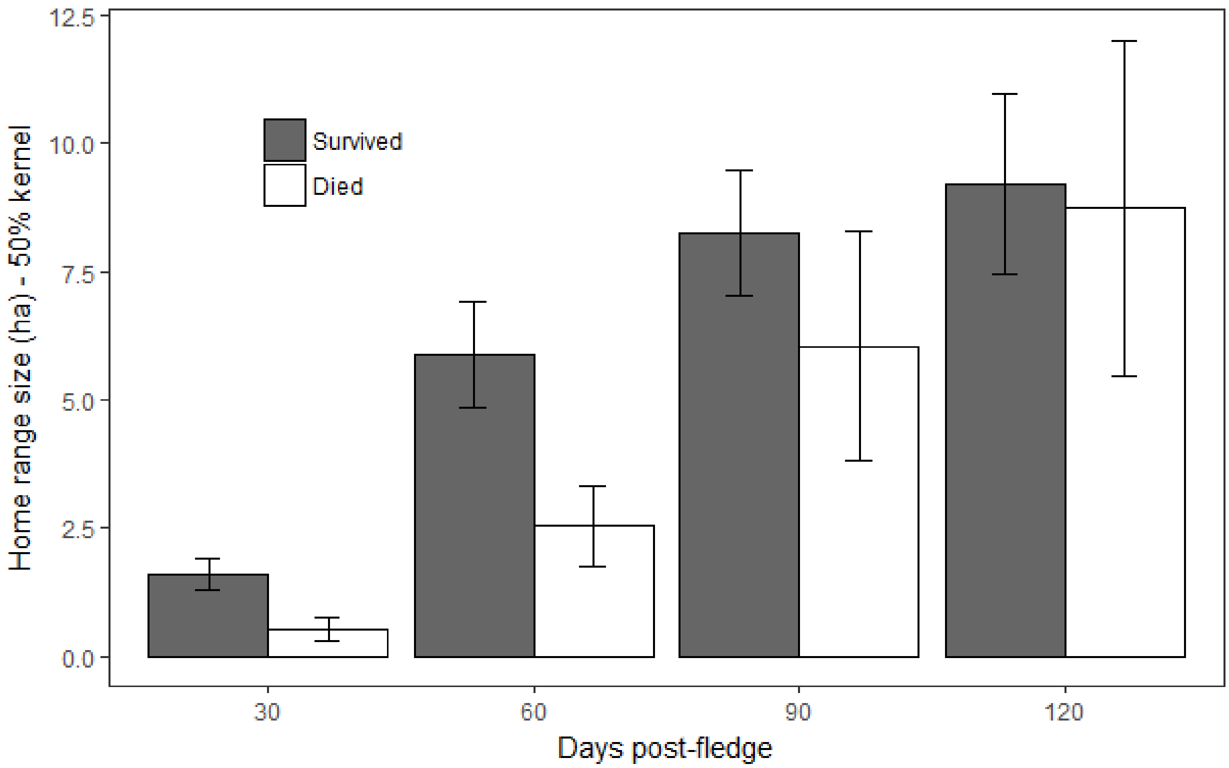

Figure 4.2: 50% core area (cumulative) in birds that survived versus died during their first year post-fledging

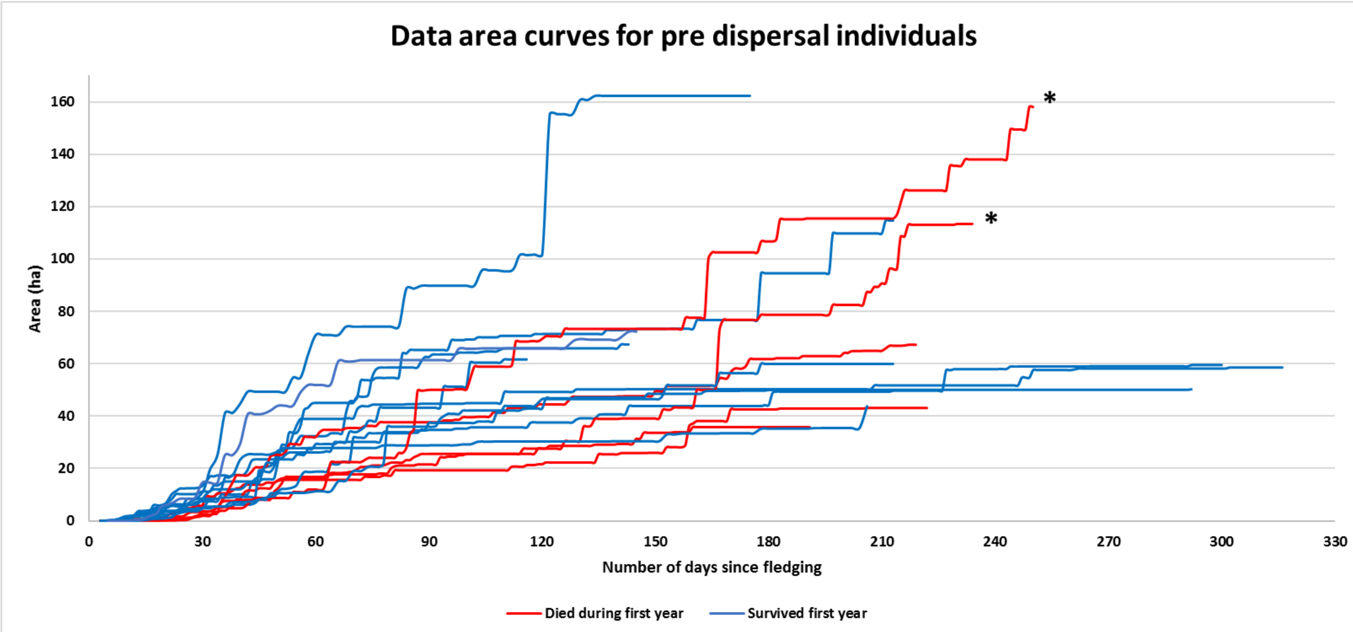

Figure 4.3: Data-area curves for the entire pre-dispersal period of fledglings who died versus survived their first year. Area curves marked with * have increases associated with the loss of one parent and search for new mate (other ranges had two parents throughout).

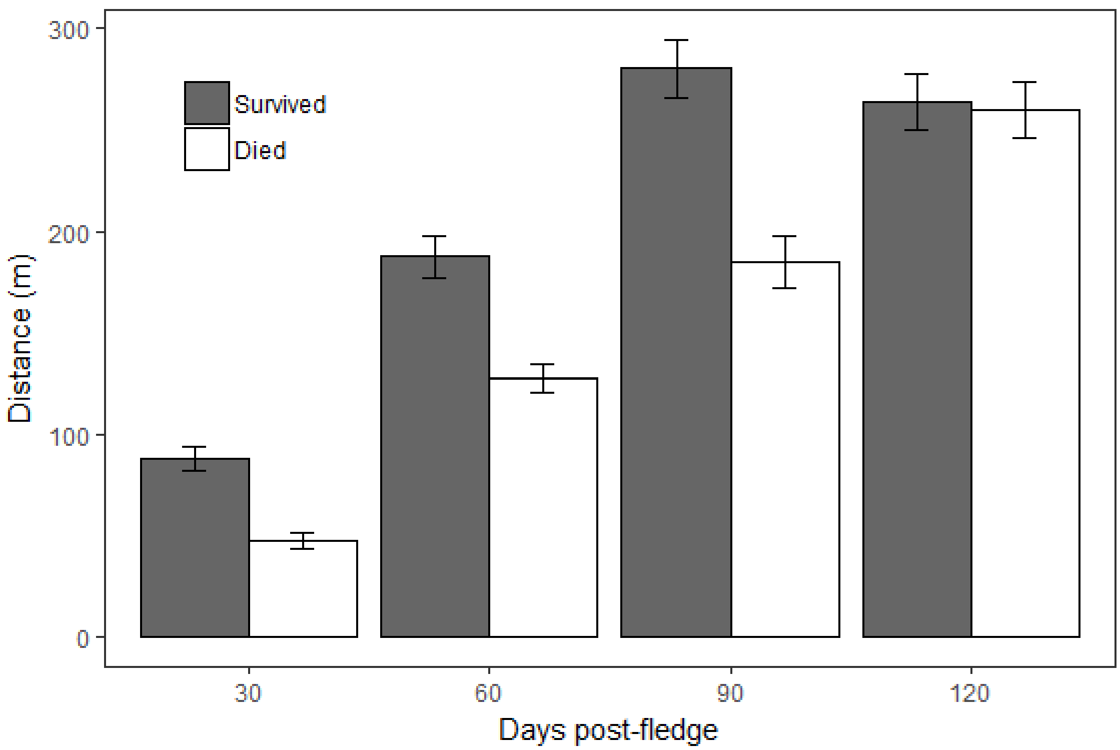

Figure 4.4: Daily movements during the first 120 days post-fledging for individuals that died vs. survived

Tables

Table 1. Causes of Death in Radio-tagged Juvenile Mariana Crows

Bird ID	**Age at death or capture for rehab (d post-fledge)**	**Cause**
84477236	15	Hepatitis (National Wildlife Health Center- Honolulu Field Station necropsy, 2010)
84477243	39	Unknown- carcass not found
84477218	51	Unknown- carcass not found
99403011	63	Probable cat predation
84477232	92	Probable cat predation
99403012	185	Probable cat predation
99403013	192	Probable cat predation
84477240	220	Unknown- carcass decayed and scavenged
84477248	222	Loss of flight due to severe feather damage and possible injury; taken into captivity for rehabilitation
84477234	234	Probable cat predation
84477238	313	Probable cat predation
99403007	349	Probable cat predation

Table 2. Pearson Product Moment Correlations in Fledgling Aga.

Measurements	***r***	***n***	***p***
Home range and daily movement	0.565	15	*0.028
Mass and wing	0.577	19	*0.01
Wing and daily movement	0.652	13	*0.016
Mass and daily movement	0.115	13	0.709
Wing and home range	0.513	15	*0.05
Mass and home range	0.227	15	0.416

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