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

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Abstract

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The Mariana Crow (*Corvus kubaryi*) is a critically endangered, island-endemic corvid whose single remaining population is on the island of Rota, CNMI. Quantitative information on the Mariana Crow's diet is lacking and the effects of age and season on diet and foraging behavior are unknown. Most corvids are social omnivores that typically learn from adults to master complex foraging behaviors. We hypothesized that age-related differences in the diets and foraging behaviors of Mariana Crows would occur due to both a period of physical maturation and steps in learning. This study identified 619 food items taken by 36 wild crows and determined the corresponding foraging strata and substrates for 469 and 363 items respectively. Fourteen percent of food captures were plant-based and 86% were animal prey; 65% of animal prey were insects or their larvae and eggs. The study also identified 209 food items, and their corresponding forest strata and substrates, taken by two captive-reared crows during the first eleven months post-release. Comparisons of the foraging behaviors and diets of captive-reared and wild crows indicated that the released crows foraged on all important prey types taken by wild crows; however, several differences in food category proportions were noted. Data from wild crows were analyzed for the effects of age class on two categorical variables: food category and foraging strata, as well as the effects of season on food category. No effect of season was detected; there was, however, a strong association between age class and food category and a moderate association between age class and foraging strata. Two food categories, fruits/seeds/plants and ants/termites/larvae, which were procured and processed with simple behaviors, were taken more frequently by fledglings. Crabs, which were processed using complex behaviors, were captured more frequently by adults. Adults acquired more food items from the ground than other age classes, a result that was driven by their high levels of crab predation. These results highlight vulnerabilities resulting from foraging behavior and may also be useful in assessments of habitat quality and the design of diets and enrichment opportunities for captive crows.

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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 and 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 and Moore 2003, Natasha Vanderhoff and 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 and 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. 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*. in press). Little evidence is available to support the theories, 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 super canopy (Tomback 1986). Previous studies have identified common food items as insects (grasshoppers, mantids, earwigs, and lepidopteran larvae), small vertebrates (lizards, immature rats, bird eggs, and nestlings), hermit crabs, and plant-based items such as fruits, seeds, flowers, foliage, 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.

The seasonal change in weather is an additional factor that 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. We hypothesized that this seasonal weather pattern would correlate with prey abundance, leading to changes in prey consumed by Mariana Crows.

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). 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 wild, radio-tagged Mariana Crows. All crows were identified as fledglings, sub-adults, or adults (defined in Table 1). Our sample included 21 radio-tagged Mariana Crows and at least 15 untagged crows. 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), were 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 come from 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. 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.

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 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 predations, 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 so rare that an estimation of time would not be meaningful.

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-based 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 (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.

The captive-reared crows' food captures were different from wild birds in some respects and they often differed from each other as well (Figure 4). 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 a higher percentage food items from the ground (33%) than GU248 (27%), though neither took as high a percentage from the ground as the wild adults (41%).

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 had not been previously reported 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, verbally 2013).

Mariana Crows foraged in a wide variety of forest substrates, frequently targeting dead or decaying plant material. Adult insects, particularly *Ensifera* species were often captured from rolled, dead leaves in the understory; ant and termites 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. It is notable that four wild Mariana Crows, taken into captivity for rehabilitation as sub-adults or adults, 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 take into account 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. Prey capture that required the most complex behaviors or fine motor skills occurred more frequently in older birds, suggesting that the differences may result from physical maturation and steps in learning. 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.).

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 and St. Clair 2012). Similarly Mariana Crows often appear unaware of their surroundings while processing food items low or on the ground, and sometimes fail to detect an approaching human observer (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 and Hokey 2008, Olson and Rauzon 2011). Many *Corvus* species habitually crack hard-shelled food items, such as nuts, by dropping them on hard surfaces (Cristol and Switzer 1999, Hunt *et al*. 2002); however this behavior has only been observed once in the Mariana Crow (T. San Nicholas, verbally 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, verbally 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 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 and 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 that may have been caused by a historical increase in crab predation.

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 were able to forage successfully on all prey types common in the diets of wild crows. However, the results also indicated potential weaknesses that could be addressed prior to the release of additional crows. The captive crows' high frequencies of wasp nest predation and low frequencies of fruit and lizard predation 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 the majority 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, H. Fandel and D. Wiitala, verbally 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 and 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, this study also has 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 close 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. Crabs made up 20% of food items captured by adults in this study, and probably made up more than 20% in terms of food weight and caloric value. Predation of hermit crabs may put crows at higher risk for feral cat predation, due to increased time spent foraging on the ground. A suspected increase in hermit crab availability in the late 1970s, following the control of *A. fulica*, may have further increased ground-based foraging behaviors in crows. 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

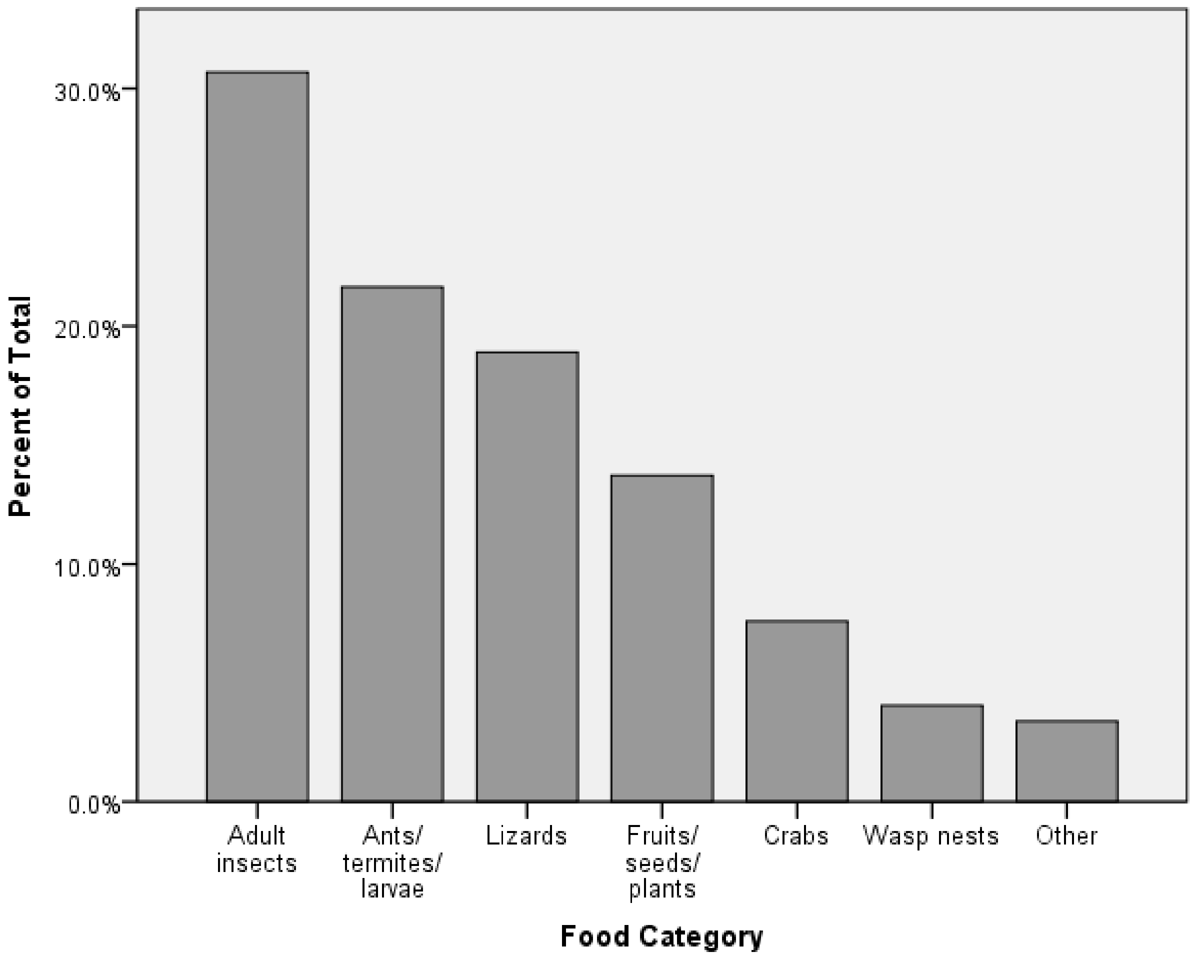

Figure 1: Frequency distribution of food categories for all ages combined

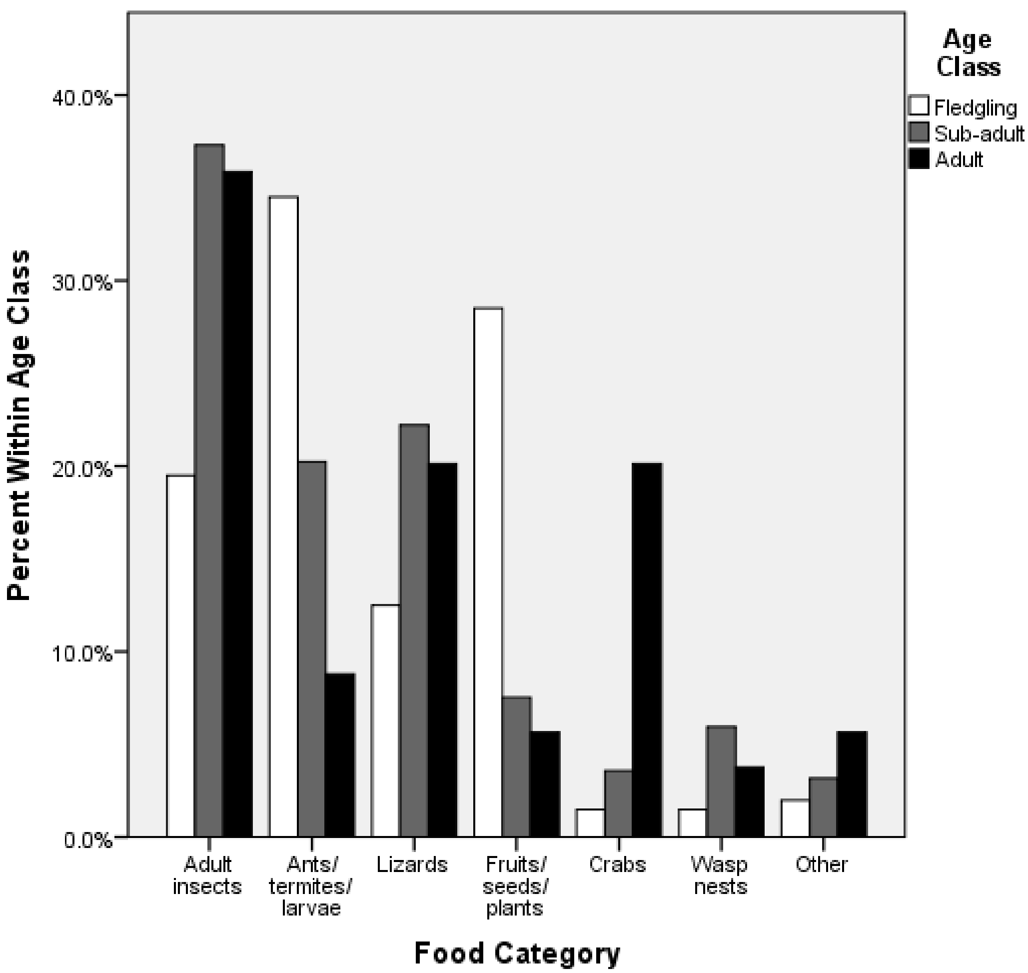

Figure 2: Percentage of food categories captured by wild fledglings, sub-adults, and adults

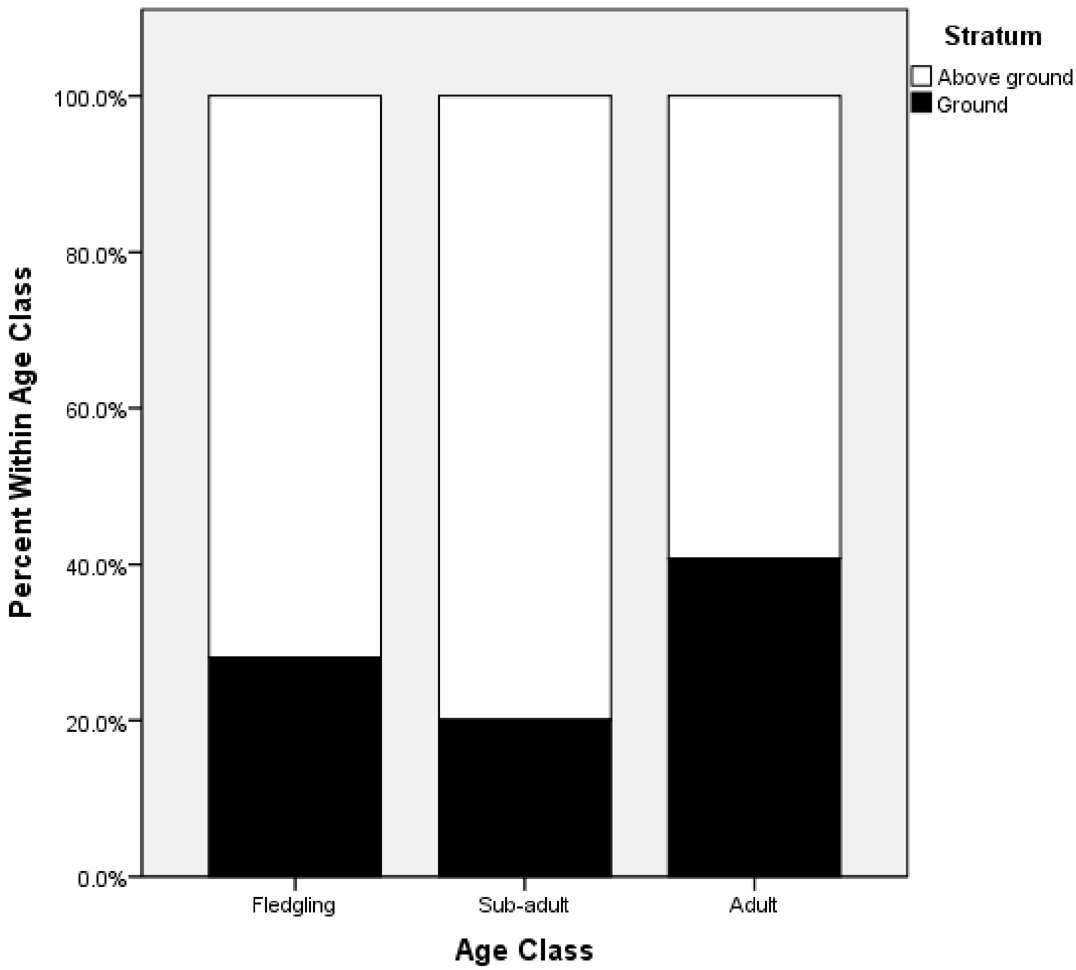

Figure 3: Percentage of food items captured from ground vs. above ground by wild fledglings, sub-adults, and adults

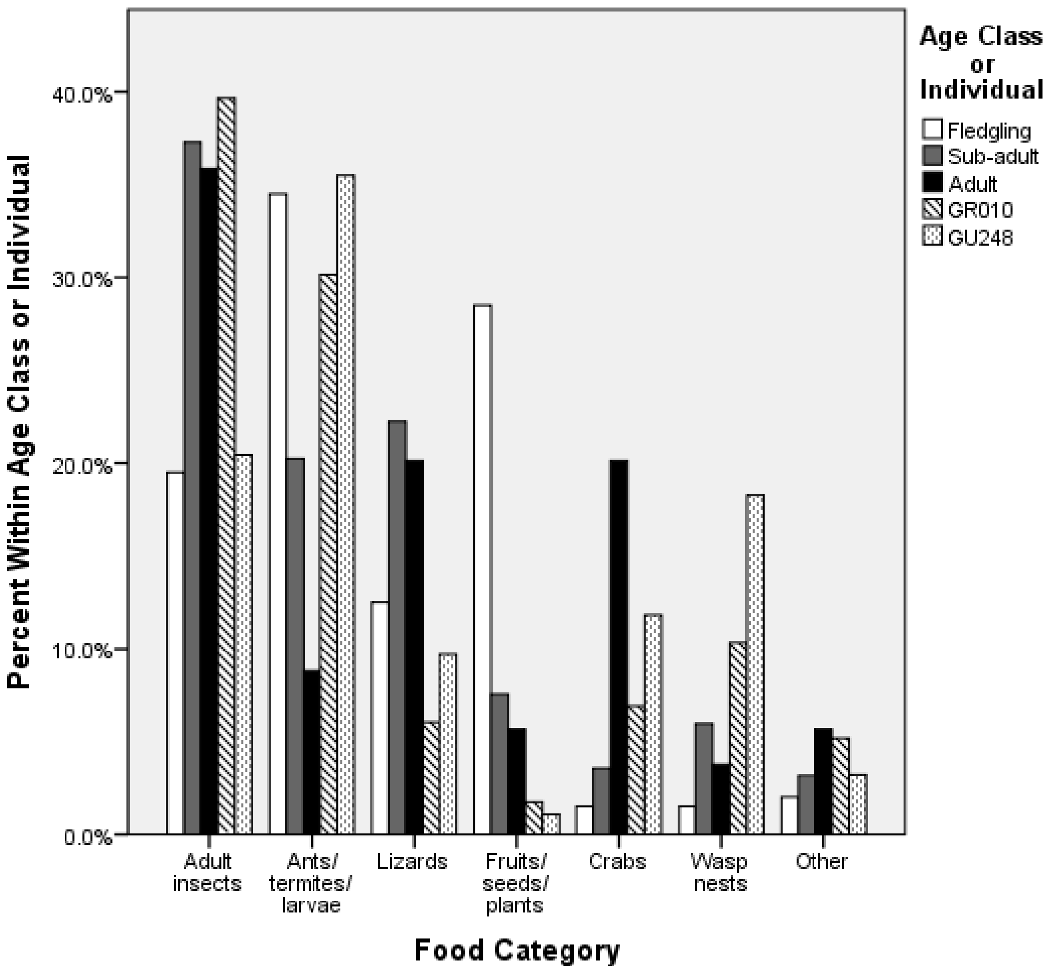

Figure 4: Percentage of food categories captured by wild and captive-reared crows

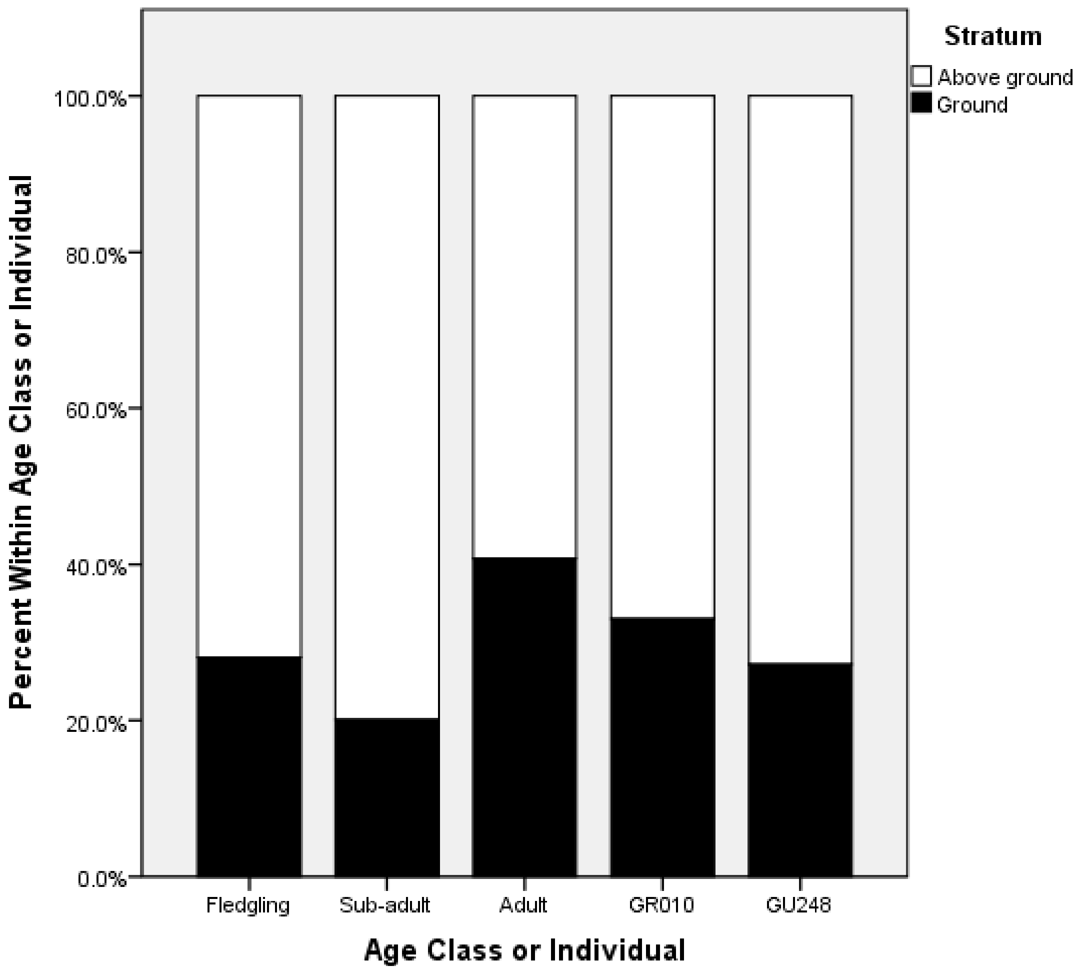

Figure 5: Percentage of food items captured from ground vs. above ground by wild and captive-reared crows

Tables

Table 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 2. Mariana Crow food category definitions

Adult insects	All adult insects except those belonging to *Termitoidae* or *Formicidae*
Termite or ant colonies or insect larvae (termites/ants/larvae)	Adults insects belonging to *Termitoidae* and *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 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 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 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 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 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 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**

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