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ORIGINAL ARTICLE

Age-related differences in diet and foraging behavior of the critically endangered Mariana Crow (*Corvus kubaryi*), with notes on the predation of *Coenobita* hermit crabs

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Abstract

Knowledge of foraging behavior across life stages of endangered species is important for identifying potential drivers of age-dependent mortality. Juvenile mortality is a primary threat to the persistence of the single remaining Mariana Crow (*Corvus kubaryi*) population, which is found on Rota, Commonwealth of the Northern Mariana Islands. Therefore, variation in foraging behavior among fledglings, sub-adults and adults may highlight different needs or susceptibilities that could inform age-specific management strategies. During observations of 36 Mariana Crows, we found that of all food captures, 14% were plant-based, 56% were insects or their larvae and eggs and 30% were non-insect animal prey. 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 did fledglings and sub-adult birds, a result that was driven by the former's high level of crab predation. We did not detect differences in foraging behavior between wet and dry seasons, suggesting that Mariana Crows maintain a similar diet year-round. Overall, our results highlight age-related differences in foraging behavior; however, future studies should identify whether these differences drive age-dependent variation in survivorship. Finally, we suggest that complex trophic interactions between non-native snails and *Coenobita* hermit crabs may have modified Mariana Crow foraging behavior, increasing their vulnerability to feral cat predation.

Keywords *Coenobita* · Anti-predator vigilance · Endangered species · Corvid · Feral cat

Zusammenfassung

Altersabhängige Unterschiede in der Ernährung und dem Nahrungssuchverhalten bei der stark gefährdeten Guamkrähe (*Corvus kubaryi*) unter Berücksichtigung der Prädation der Landeinsiedlerkrebs-Gattung *Coenobita*

Kenntnisse über das Nahrungssuchverhalten verschiedener Lebensstadien bei gefährdeten Arten sind notwendig, um potentielle Einflussfaktoren auf die altersabhängige Mortalität zu identifizieren. Die Sterblichkeit von Jungtieren ist eine

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der größten Bedrohungen für den Fortbestand der einzig verbliebenen Population an Guamkrähen (*Corvus kubaryi*) auf der Insel Rota, Commonwealth der Nördlichen Marianen. Unterschiede im Nahrungssuchverhalten zwischen flüggen Jungvögeln, subadulten und adulten Vögeln könnten verschiedene Ansprüche oder Gefährdungen hervorheben, die dann in altersabhängige Managementstrategien einfließen könnten. Während der Untersuchung von 36 Guamkrähen fanden wir heraus, dass 14% der aufgenommenen Nahrung pflanzlich war, 56% aus Insekten oder deren Larven und Eiern bestand und 30% aus anderer tierischer Beute. Die zwei Nahrungskategorien Früchte/Saaten/Pflanzen und Ameisen/Termiten/Larven, welche auf einfache Art und Weise zu beschaffen und bearbeiten sind, wurden häufiger von flüggen Jungvögeln aufgenommen. Krebse, dessen Handhabung eines komplexen Verhaltensmusters bedarf, wurden häufiger von adulten Vögeln gefangen. Adulte Vögel sammelten im Vergleich zu den anderen Altersklassen mehr Nahrung vom Boden, ein Ergebnis, dass vermutlich aufgrund des hohen Krebsanteils in der Beute zustande kam. Wir konnten keine Unterschiede im Nahrungssuchverhalten zwischen Regen- und Trockenzeiten entdecken, was auf eine ganzjährig gleichbleibende Ernährung der Guamkrähe schließen lässt. Zusammenfassend zeigen unsere Ergebnisse altersabhängige Unterschiede im Nahrungssuchverhalten auf. Jedoch sollten zukünftige Studien herausfinden, ob diese Unterschiede die altersabhängigen Variationen in der Überlebensrate verursachen. Schließlich gehen wir davon aus, dass komplexe trophische Interaktionen zwischen nicht einheimischen Schnecken und den Landeinsiedlerkrebsen der Gattung *Coenobita* das Nahrungssuchverhalten der Guamkrähe verändert haben, was zu einer Zunahme der Gefährdung der Krähen durch verwilderte Hauskatzen geführt hat.

Introduction

Animals are expected to optimize their foraging effort so that nutritional benefits outweigh energetic costs (Pyke et al. 1977). Optimal foraging strategies can vary across life stages (Engen and Stenseth 1989) due to variation in nutritional needs (Partridge and Greene 1984), 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; Marchetti and Price 1989; Wunderle 1991; Heise and Moore 2003; Vanderhoff and Eason 2008) and rely on foods that are the easiest to procure (Yoerg 1994). 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).

Age-related foraging behavior is an important factor to consider in bird studies because most bird species experience age-dependent mortality, with younger individuals being more susceptible to starvation and predation (Lack 1954; Sullivan 1988; Martin 1995). Studies of the diets and foraging behaviors of endangered species may highlight age- or season-specific needs or vulnerabilities (e.g. Smith-Hicks et al. 2016; Price and Hayes 2017) and may help wildlife managers predict responses to changes in the availability of food resources.

Oceanic island birds are among the most threatened groups of species worldwide, largely due to the introduction of non-native predators and habitat alteration (Steadman 2006). Understanding the foraging strategies of island birds may reveal vulnerabilities to non-native predators, since foraging trades off with anti-predator vigilance (Lawrence 1985; Dukas and Kamil 2000), and island birds generally evolved in the absence of cursorial predators. Additionally, 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). Thus, information on diet and foraging behavior may be used to improve predictions of species' responses to global change.

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). Between 1982 and 2012, the Mariana Crow population declined by 95% (Camp et al. 2015) and mitigation of juvenile mortality has become a primary management objective (Ha et al. 2010). Evidence from radio-telemetry studies suggests that predation by feral cats (*Felis catus*) is one cause of mortality (S. Faegre and R. Ha, unpublished data). A poorly understood inflammatory disease is also responsible for the deaths of immature birds (T. Work, unpublished data).

Mariana Crows are opportunistic generalists that take advantage of both native and non-native food sources within primary and secondary limestone forest, using all forest strata, from ground to supercanopy (Tomback 1986). Mariana Crow family groups (3–4 individuals; Faegre et al. 2018) have dynamic, shifting home ranges, and members forage primarily alone or in family groups.

Previous studies have identified the most common food items to be insects, including Ensifera (grasshoppers and crickets), Mantodea (mantids), Dermaptera (earwigs) and Lepidoptera (moths and butterflies) larvae; small vertebrates, including Lacertilia (lizards), immature *Rattus* (rats) and *Aves* (birds) eggs and nestlings; *Coenobita* hermit crabs; and plant-based items, such as fruits, seeds, flowers and bark (Beaty 1967; Jenkins 1983; Tomback 1986; Michael 1987; Nietmann and Ha 2018). However, quantitative information on diet is lacking, and the effects of age and season on diet and foraging behavior are unknown.

In the study reported here, we describe the diets and foraging behaviors of wild crows during three life stages (fledgling, sub-adult and adult). We predicted adults would more frequently capture crabs, which are processed using a complex sequence of behaviors, while fledglings would more frequently obtain plant-based items that can be taken and processed using fewer or simpler movements (S. Faegre, personal observation). We then compared the frequencies with which the three age classes captured food items from two foraging strata, namely, the ground (where items from all food categories can be found) and above ground (where items from all except the 'crabs' category of food items can be found), since ground-based foraging may increase susceptibility to feral cat predation. We also compared Mariana Crow diets between wet and dry seasons, because seasonal weather patterns can drive changes in foraging behavior in tropical birds (Jahn et al. 2010). Finally, we identified native and non-native components of the diet and describe a complex trophic interaction between non-native snails, *Coenobita* hermit crabs and 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. Monthly rainfall ranges from a minimum of 93.7 mm in March to a maximum of 339.6 mm in September (Lander and Guard 2003). 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

Between March 2010 and March 2013, we conducted daily observations of 21 wild, radio-tagged Mariana Crows and at least 15 untagged crows for a total of 254 h. All untagged crows were parents or mates of 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 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 a nesting attempt (i.e. caring for fledglings) was observed. The precise number of adults in this study is unknown, since many individuals were not color-banded. However, based on the number of family groups in which unbanded and/or banded adults were observed capturing food, our data cover a minimum of 17 adult crows.

Tagged crows were located daily using radio-telemetry and observed from a distance of 2–10 m, using 8 × 42 or 10 × 42 binoculars as needed. 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 to 150 min with a median of 23 min.

Table 1 Mariana Crow (*Corvus kubaryi*) food category definitions

Food item category	Description of food item category
Adult insects	All adult insects except those belonging to Isoptera: Termitoidae or to Hymenoptera: Formicidae
Ants/termites/larvae	Adults insects belonging to Hymenoptera: Formicidae and to Isoptera: Termitoidae; and to larvae or eggs of any insect
Wasp nests	*Polistes* wasp larvae
Lizards	Animals of the suborder Lacertilia
Crabs	Animals of the order Brachyura
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

Food items were categorized based on taxonomy and foraging technique (Table 1). Since it was not possible to determine the quantity of some food items, only 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 min apart), then food items were treated as being independent from one another. If food items were not independent, a single item was selected randomly from those taken in a given 10-min block to use in subsequent analyses.

For each foraging observation, we categorized forest strata depending on whether the food item was procured on the forest floor or on fallen logs (hereafter 'ground') or above this stratum ('above ground'). We further categorized foraging substrate to assess foraging habitat use at a finer scale (Table 2). *Pandanus* trees were placed in a separate category from other foliage because foraging crows often target *Pandanus* (Jenkins 1983) and use unique foraging techniques (shredding or tugging at leaf bases, or piercing leaves) to access hidden prey within them (S. Faegre, personal observation). Finally, we compared observations occurring during the wet season (July–November) with those occurring during the dry season (January–May).

Statistical analyses

All statistical analyses were conducted using SPSS 19 (IBM Corp. 2010). Log-linear analysis was not used because the study design was not fully factorial, since one of the food categories (crabs) was found only on the ground. We used three Pearson's Chi-square tests to evaluate 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, we set alpha at 0.05 and used a family-wise alpha of 0.01 for the three primary Chi-square tests. We also conducted all pairwise comparisons of food category and age class using additional 2×2 Chi-square tests. The Bonferroni correction was applied to pairwise comparisons and alpha was set at 0.002. For tests of the relationship between (1) age and food type and (2) age and forest stratum, we also calculated the strength of association.

Results

This study identified 619 food items taken by 36 wild crows (Table 3) and determined the corresponding foraging strata and substrates for 469 and 363 items, respectively. Of all food captures, 14% were plant-based foods, 56% were insects or their larvae and eggs and 30% were non-insect animal prey. Adult insects were the most frequently captured food category within each age class and made up 31% of food items overall (Fig. 1). A variety of non-native species were included in the diet, including *Polistes* paper wasps, a cane toad and non-native fruits. *Coenobita* hermit crab prey was native, but the individuals preyed upon by crows were housed in non-native *Achatina fulica* snail shells (Table 3).

Of all food items consumed, 95% were consumed by crows of known age, with 33% consumed by fledglings, 41% by sub-adults and 26% by adults. Fledglings and sub-adults consumed food items they procured while adults shared or fed at most food items with their offspring, if offspring were present. Therefore, while sub-adult and adult food captures accurately represent their food intake, those of fledglings do not because they were also fed by their parents. 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 4–10 months post-fledging (mean 8 months;

Table 2 Descriptions of Mariana Crow foraging substrates

Foraging substrate	Description of foraging substrate
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 alive, 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 3 Independent observations of food items taken by wild Mariana Crows

Food item	Number observed (% of total)
Adult insects (except Termitoidae or Formicidae)	**190 (30.7)**
Ensifera spp. (crickets and katydids)	103 (16.6)
Mantodea spp. (mantids)	3 (0.5)
Phasmatodea spp. (walking sticks)	1 (0.2)
Lepidoptera spp. (moths and butterflies)	1 (0.2)
Unknown adult insect	82 (13.2)
Termitoidae or Formicidae colonies and unknown insect larvae or eggs	**134 (21.6)**
Termitoidae or Formicidae colony (unspecified)	56 (9.0)
Formicidae (ant) colony	23 (3.7)
Termitoidae (termite) colony	4 (0.6)
Lepidoptera (moth/butterfly) larvae	3 (0.5)
Unknown insect egg case	3 (0.5)
Unknown insect larvae	45 (7.3)
Polistes (wasp) nests	**25 (4.0)**
Lacertilia (lizards)	**117 (18.9)**
Lacertilia spp.	5 (0.8)
Gekkonidae spp. (Geckos)	103 (16.6)
Scincidae spp. (Skinks)	9 (1.5)
Brachyura (Crabs)	**47 (7.6)**
Coenobita spp. (Hermit crabs)[a]	43 (6.9)
Birgus latro (Coconut crabs)	1 (0.2)
Other land crabs	3 (0.5)
Fruits, seeds and other plant-based items	**85 (13.7)**
Artocarpus spp. fruit	11 (1.8)
Carica papaya fruit	8 (1.3)
Cocos nucifera fruit[b]	4 (0.6)
Cordia subcordata fruit	2 (0.3)
Eleocarpus joga fruit	1 (0.2)
Eugenia spp. fruit	2 (0.3)
Ficus spp. fruit	1 (0.2)
Guamia mariannae flowers	1 (0.2)
Hernandia spp. fruit	1 (0.2)
Intsia bijuga bark	2 (0.3)
Melanolepis multiglandulosa fruit	1 (0.2)
Mammea odorata leaf stems	1 (0.2)
Mucuna spp. seed	2 (0.3)
Ochrosia mariannensis fruit	1 (0.2)
Pipturus argenteus fruit	4 (0.6)
Premna obtusifolia fruit	2 (0.3)
Psychotria mariana fruit	2 (0.3)
Scaevola sercea fruit	1 (0.2)
Triphasia trifolia fruit	32 (5.2)
Unknown fruit	5 (0.8)
Unknown seed	1 (0.2)
Other	**21 (3.4)**
Aplonis opaca (Micronesian Starling) nestling	3 (0.5)
Gallicolumba xanthonura (White-throated Ground Dove) nestling	4 (0.6)
Gygis alba (White Tern) egg	1 (0.2)
Rhipidura rufifrons (Rufous Fantail) nestling	1 (0.2)

Table 3 (continued)

Food item	Number observed (% of total)
Unknown nestling	3 (0.5)
Bufo bufo (Cane toad)	1 (0.2)
Araneae spp. (spider)	3 (0.5)
Scolopendra spp. (centipede)	2 (0.3)
Lacertilia spp. (lizard) eggs	2 (0.3)
Aricularia spp. mushroom	1 (0.2)

The values presented in bold are the total number of food items in the given food category

[a] There are five species of *Coenobita* hermit crab on Rota. *C. brevimanus* is the most common species within the limestone forests of Rota and is also the most common *Coenobita* species preyed upon by Mariana Crows (*S. Faegre*, personal observation.). *C. spinosus*, *C. cavipes* and *C. perlatus* are also commonly found in the crow's habitat, while *C. rugosus* is found mainly on shores

[b] 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*) or that had been left in farms for livestock. These observations have management implications since there is a risk of human persecution (Sussman et al. 2015) when crows take food that is intended for livestock

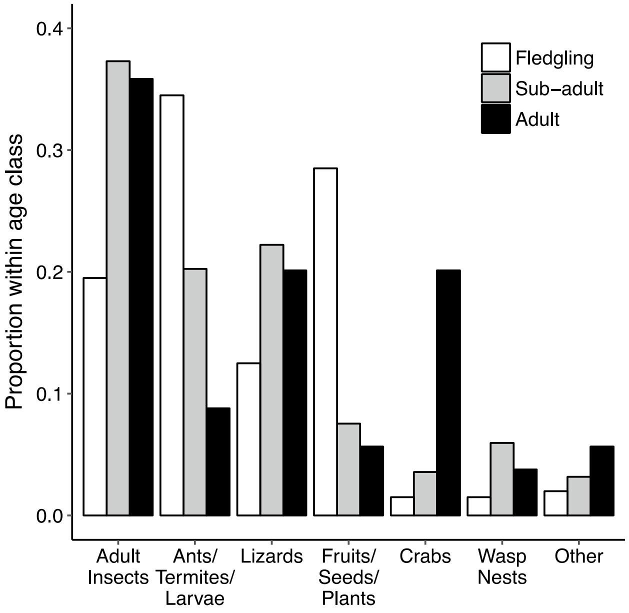

Fig. 1 Fledgling, sub-adult and adult Mariana Crow (*Corvus kubaryi*) food capture frequencies

$n = 13$). The recruitment of one sub-adult into the breeding population occurred at 16 months post-fledging, which is the youngest documented recruitment of a Mariana Crow.

Due to variation in age at dispersal, there was some overlap in absolute age (in days post-fledging) between the fledgling and sub-adult categories. The mean (± standard deviation) age of Mariana Crows during observed food captures was 170 ± 68 days post-fledging (range 10–293 days) for fledglings, and 302 ± 66 days post-fledging (range 122–462 days) for sub-adults. Most adults were not banded and their exact ages were unknown.

Crows captured animal prey from all forest substrates. 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 4). Since descriptions of substrate were absent from 41% of food captures, Table 4 presents the minimum numbers of items from each food category taken from each substrate.

We found a strong association between age class and food type ($\chi^2_{12} = 151.59$, $n = 611$, $P < 0.001$, $V = 0.352$; Fig. 1). Fledglings took more fruits/seeds/plants than adults ($\chi^2_1 = 30.80$, $n = 359$, $P < 0.001$) or sub-adults ($\chi^2_1 = 35.02$, $n = 452$, $P < 0.001$), with the frequency decreasing from 29% in fledglings to 8 and 6% in sub-adults and adults, respectively. Adults captured more crabs than fledglings ($\chi^2_1 = 34.93$, $n = 359$, $P < 0.001$) or sub-adults ($\chi^2_1 = 29.75$, $n = 411$, $P < 0.001$), with the frequency increasing from 2 and 4% in fledglings and sub-adults, respectively, to 20% in adults. Based on timed observations of hermit crab predation events, adults spent 3–7 min (mean 4.4 min; $n = 6$) opening hermit crabs while sub-adults spent 9–24 min (mean 17.6; $n = 3$). Hermit crab predation was rare among fledglings, and timed observations were not available for this age class.

Additional pairwise comparisons suggested fledglings captured more ants/termites/larvae than sub-adults ($\chi^2_1 = 11.63$, $n = 452$, $P = 0.001$) or adults ($\chi^2_1 = 32.90$, $n = 359$, $P < 0.001$) and that sub-adults captured more ants/termites/larvae than adults ($\chi^2_1 = 9.57$, $n = 411$, $P = 0.002$; Fig. 1). The frequency of predation on ants/termites/larvae decreased, from 35 to 20 to 9% in fledglings, sub-adults, and adults respectively. Fledglings captured fewer adult insects than adults ($\chi^2_1 = 12.09$, $n = 359$, $P = 0.001$) or sub-adults ($\chi^2_1 = 17.02$, $n = 425, P < 0.00$; Fig. 1). Sub-adults trended

Table 4 Frequencies of foraging substrates within food categories taken by wild Mariana Crows

Foraging substrates	Adult insects	Ants/termites/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

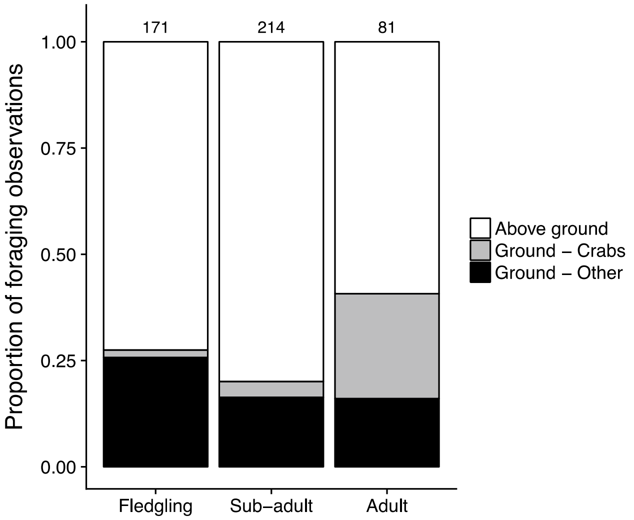

Fig. 2 Proportion of foraging observations of known-age Mariana Crows that occurred above ground, on the ground for crabs, and on the ground for all other food types. Numbers above bars indicate total number of observations for each age class

towards capturing more lizards than fledglings (χ_1^2 = 7.17, $n = 452$, $P = 0.007$) and more wasp nests than fledglings (χ_1^2 = 5.78, $n = 452$, $P = 0.016$); however, these results were not significant at the level of the Bonferroni-adjusted alpha.

There was a moderate association between age class and forest strata (χ_2^2 = 13.12, $n = 466$, $P = 0.001$, $V = 0.168$; Fig. 2). Pairwise comparisons showed that adults obtained more food from the ground than did sub-adults (χ_1^2 = 13.10, $n = 295$, $P < 0.001$) and tended to capture more food from the ground than fledglings ($\chi_1^2 = 4.05$, $n = 252$, $P = 0.044$). However, when captures of crabs were removed from the analyses, the relationship between age class and foraging strata disappeared ($\chi_2^2 = 5.28$, $n = 435$, $P = 0.071$, $V = 0.110$; Fig. 2).

We found no evidence of seasonal differences in food category frequencies, ($\chi_6^2 = 2.51$, $n = 531$, $P = 0.87$). 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.

Discussion

Age-related differences in Mariana Crow foraging behavior followed a pattern similar to that observed in other species that learn complex foraging skills (Yoerg 1994; Holzhaider et al. 2010a, b). More difficult foods, which require correct sequencing of discrete behaviors and/or the use of fine motor skills, were consumed more frequently by older birds, suggesting that the differences may result from physical maturation and steps in learning. The capture and processing of hermit crabs requires a complex sequence of movements, culminating in a rapid shaking behavior not employed in other types of foraging (S. Faegre, personal observation, Electronic Supplemental Material [ESM] Video 1). By contrast, the fruits/seeds/plants and ants/termites/larvae categories contain foods that are easier to procure, requiring repetition of only a few, simple movements. Although animal prey accounted for 86% of all foraging observations (Table 3), plant-based foods were an important food source, especially during the fledgling period. The wide variety of native fruits consumed (Table 3) suggests crows play a role in seed dispersal.

Adult Mariana Crows captured more food items from the ground than did fledglings and sub-adults due to their increased frequency of crab predation (Fig. 2). However, this higher frequency of ground-based food captures in adult crows may not be indicative of total time spent on the ground. On average, sub-adults took fourfold longer than adults to break open hermit crab shells. Sub-adults were also observed making unsuccessful attempts at crab predation while adults never failed to open a crab. Fledglings often followed their parents closely during foraging, especially during food processing (S. Faegre, personal observation), and the time they spend on the ground may mirror that of their parents.

Ground-based foraging has important conservation implications. The Mariana Crow evolved without any natural predators and may have been subject to relaxed selection for anti-predator behaviors, as has been observed in other island endemic animals (Blumstein 2002; Blumstein et al. 2004; Rutz and St. Clair 2012). Interestingly, New Caledonian Crows (*Corvus moneduloides*) also frequently engage in ground-based foraging, suggesting that this behavior may be common in island corvids (Rutz et al. 2007). Mariana Crows sometimes failed to detect an approaching human observer while processing food items near or on the ground (S. Faegre, personal observation). Hermit crab predation is a complex behavior that may require reduced vigilance, since there is risk of injury if a crow is not focused on its prey (S. Faegre, personal observation). For example, in two studies, vigilance behavior in Blue Jays (*Cyanocitta cristata*) and Common Blackbirds (*Turdus merula*) was found to be reduced when the birds were processing difficult food items, as compared to easier items (Lawrence 1985; Dukas and Kamil 2000). While Mariana Crows respond appropriately when they detect a predator (e.g. feral cat), reduced vigilance behaviors may increase their vulnerability to feral cat predation while processing hermit crabs on the ground.

Processing of hermit crabs

Mariana Crow hermit crab processing was comprised of three suites of behaviors: (1) placement of the shell in a stable position, (2) breaking the shell and (3) removal of the crab abdomen (ESM Video 1). The sequence and strategies varied among age classes and individuals, with greater consistency among wild adults. In wild adults, step one was completed quickly, usually by wedging the shell against a rock, root or fallen branch, after which crows pecked forcefully at shells, 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 carapace and abdomen and shaken rapidly from side to side until the abdomen separated (S. Faegre, personal observation).

Fledgling Mariana Crows watched conspecifics 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, personal observation, ESM Video 2). New Caledonian Crows and Common Ravens (*Corvus corax*) rely on social learning and/or trial and error for the development of complex foraging behaviors (Fritz and Kotrschal 1999; Bluff et al. 2010; Holzhaider et al. 2010a, b). Similarly, the crab processing skills of five captive-reared Mariana Crow fledglings developed gradually over a period of 1–2 years (S. Faegre, unpublished data), likely resulting from both trial-and-error and social learning.

Frequent predation of *Coenobita* hermit crabs by Mariana Crows is unique among *Corvus* species, and also among most land birds. In particular, the 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 2009; 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 Mariana Crows (T. San Nicholas, personal communication, 2014).

Coenobita species in forested areas of Rota primarily use shells of the introduced Giant African Land Snail (*Achatina fulica)* and those of the native Rough Turban (*Turbo setosus*) shells. Crows almost exclusively preyed upon hermit crabs occupying the relatively weak *A. fulica* shells (100% of hermit crab predation events observed in this study). Although there have been two observations of crows removing *Coenobita* hermit crabs from the harder *T. setosus* shells, neither observation involved the crow breaking the shell (H. Fandel, personal communication, 2014).

Coenobita hermit crab populations are limited by shell availability (Hazlett 1981). We speculate that the 1930s introduction of *A. fulica* to Rota, and the subsequent biological control of *A. fulica* in the 1970s (National Research Council U.S. 1954; Nafus and Schreiner 1989) may have indirectly impacted Mariana Crows by increasing the availability of *Coenobita* hermit crabs to crows. *Coenobita* hermit crabs are rich in nutrients and high in fat (Lawrence 1976). While an increase in crab availability would have provided some nutritional benefits to the crow population, an increase in ground-based foraging for crabs could also have carried increased predation risks for crows.

Conclusions

Fledglings and sub-adults captured adult insects and crabs at a lower rate than adults and fed more frequently on ants/termites/larvae and fruits. While fruit- and larva-heavy diets in fledglings are supplemented by their parents' food-captures, sub-adults may be at increased risk for nutritional stress if easy-to-procure food items are limited. Adult Mariana Crows capture more food items from the ground than do fledglings or sub-adults (Fig. 1). However, fledglings and sub-adults may spend equal or more time engaged in ground-based foraging, given the inefficiency with which fledglings and sub-adults execute complex foraging maneuvers required to capture and process hermit crabs. Future studies should compare the time budgets and vigilance behaviors of fledglings, sub-adults and adults to better understand the relationship between ground-based activities and age-related vulnerabilities. Given that Mariana Crows forage on the ground for much of their sustenance, while showing signs of reduced vigilance, continuing a program of mortality monitoring to better understand the role of cat predation is imperative.

The hypothesis that the introduction and subsequent biological control of thin-shelled *A. fulica* resulted in an increase in crab availability (leading to a correlated increase in ground-based foraging by Mariana Crows) warrants further study. We recommend the use of stable isotopes to compare the importance of crabs in the diet of Mariana Crow specimens collected before and after the introduction of *A. fulica*. Very little is known about the foraging behaviors of other tropical Australasian crows that are likely candidates for hermit crab predation behaviors; observations of some of these species could also lead to a better understanding of hermit crab-foraging behaviors in the absence of *A. fulica* shells.

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