

Foraging Decision Rules and Prey Species Preferences of Northwestern Crows (*Corvus caurinus*)

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Abstract

Categorization of similar prey types and the application of decision rules by dietary generalists can enhance the efficiency of foraging decisions and facilitate the inclusion of novel prey types in the diet. While considerable research attention has been directed toward investigation of these concepts in invertebrates, few have assessed categorization and decision rules used by generalist vertebrate predators. In this study, we experimentally investigated decision rules and prey preferences of northwestern crows (*Corvus caurinus*) feeding on littleneck clams (*Tapes philippinarum*) and whelks (*Nucella lamellosa*). We presented crows with three species-size combinations: small clams (2.0–2.9 cm length) paired with large whelks (4.0–4.9 cm), small clams paired with medium whelks (3.0–3.9 cm), and large clams (4.0–4.9 cm) with large whelks. Profitability estimates based on observations of crows feeding on these prey species indicated that clams were always the more energetically profitable option; however, in prey choice trials crows consistently selected the heavier prey species, regardless of differences in profitability. These results show that crows apply a general decision rule according to which they select heavier prey items when feeding on hard-shelled prey requiring similar handling techniques, and that while such decision rules may approximate optimal choices they may not always follow predictions based solely on prey profitability. We discuss these results in the context of behavioural flexibility of generalist predators, and predicting impacts of intertidal avian predators on prey populations.

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Introduction

Optimal foraging models generally assume that predators make foraging decisions based on specific cues that they can readily perceive and accurately assess,

and that serve as reliable indicators of prey quality (Stephens & Krebs 1986). Most predators apply decision rules related to physical characteristics of prey (e.g. Mitchell 1989; Heinrich et al. 1997; Langen & Gibson 1998), and under natural conditions, such decision rules tend to approximate optimal choices (Janetos & Cole 1981). Further, for consumers that encounter strong intraspecific competition while foraging, general decision rules may allow choices to be made quickly, thereby minimizing the chance of food loss by stealing (e.g. Ha & Ha 2003).

It has been argued that generalist predators should exhibit plasticity in their application of decision rules, as this would allow them to take advantage of novel resources (Micheli 1995). Such behavioural flexibility has been demonstrated in crabs feeding on clams: prey size preferences of crabs varied according to their previous experience, and appeared to be based on perceived clam shell strength, even at the expense of profitability (Micheli 1995). In addition to flexibility of prey preferences, however, it may be equally important for a generalist predator to be capable of applying a common decision rule across different prey types that present similar handling constraints. In this way, novel prey types would be initially assessed according to pre-existing rules that apply to similar known prey categories. The capacity to categorize similar food types has been demonstrated in bumblebees (Dukas & Waser 1994), and the ability of generalist predators to transfer handling skills from familiar to novel prey requiring similar handling methods has been reported in crustaceans (Hughes & O'Brien 2001). However, preferences of vertebrates presented with more than one prey type have received little research attention (but see Cristol 2001). Thus, the ability of generalist vertebrate predators to apply common decision rules across prey species and, potentially, from familiar to novel prey types, remains relatively unknown.

In the present study, we used northwestern crows (*Corvus caurinus*) feeding on littleneck clams (*Tapes philippinarum*) and whelks (*Nucella lamellosa*) to test the hypothesis that generalist predators apply a common decision rule when assessing different prey species that present similar handling constraints. Northwestern crows regularly forage in the intertidal zone and encounter both clams and whelks, which they drop on hard substrates to break open (Verbeek & Butler 1999). Previous investigations of prey size preferences of northwestern crows have shown that adult birds preferentially select larger, heavier shells when presented with a range of sizes of either clams or whelks; in both prey species, larger shells are more profitable as they require fewer drops to break open and provide a greater energetic return (Zach 1979; Richardson & Verbeek 1986). However, preferences of crows when presented simultaneously with more than one species of mollusc have not been investigated. In this study, it was predicted that crows feeding on hard-shelled molluscs would apply a general decision rule to select the heaviest prey items, regardless of prey species. Further, if this decision rule approximates the optimal solution in natural foraging situations, but is not directly based on profitability ratios of energetic yield per unit time (Bouskila & Blumstein 1992), heavier molluscs should be preferred by crows even where those items are not the most profitable choice. Avian intertidal predators can have considerable impacts on marine invertebrate populations (Wootton 1997), and

efforts to construct behaviour-based models that will allow us to predict these impacts (e.g. Stillman et al. 2000) require an understanding of decision rules applied by predators in a natural foraging context. This study provides information that will enhance our understanding of such rules for a common avian intertidal predator.

Methods

We studied prey selection of northwestern crows from Jan. to Apr. 2002 in Victoria, British Columbia, Canada (48°24'N, 123°21'W). Prey-dropping substrates at the study site included an exposed rock outcrop and shallow-sloped rocky beach approx. 500 m long. Northwestern crows regularly visited the site, foraging for invertebrates along the shore by turning over kelp and other organic material deposited above the wave zone. The birds were not marked for individual identification, and it was therefore not known if the same birds were present in each trial. Within a trial it can be assumed that the same crows rarely made multiple choices, because crows required several minutes to break open and consume both clams and whelks, and all of the preferred items were frequently removed by other crows before one individual could return to make another selection. Thus, observations in each trial represented the collective decisions made by several crows, each making a single selection from the feeding platform. Trials in which one or more birds were known to have made repeated selections (i.e. where only one or two birds were present) were omitted from the analysis. As several hundred crows roosted and foraged in the vicinity of the study site, there was a low probability that the same individuals repeatedly participated in feeding trials across trial days.

Clams and whelks used in feeding trials were collected during low tide at an intertidal site on southeastern Vancouver Island. We began the feeding trials at dawn, when crows actively foraged along the beach. Consequently, trial start time varied from 0830 h PST in Jan. to 0530 h PST in Apr. As crows rarely visited the beach or dropped prey when exposed to strong rain or wind, we limited trials to mornings with little to no wind or precipitation. In all trials, we presented invertebrate prey items on a 60 × 90 cm plywood feeding platform at the same location on the beach, above the high-tide line. Although northwestern crows begin nesting as early as Mar. (Verbeek & Butler 1999), the provisioning area was not located within a defended territory and thus, no birds were excluded from foraging at the platform by territorial breeding pairs. We randomly located prey items on a grid drawn on the platform, and made behavioural observations from a distance of 10 m. It is unlikely that foraging behaviour was influenced by observer proximity, as crows at the site were accustomed to human presence.

Profitability Estimates

We divided handling time for crows feeding on clams and whelks into three behavioural components, including flying, standing and walking. Shell length of

clams and whelks (apex to siphonal canal of whelks; longest shell axis of clams) was measured to the nearest millimeter with vernier calipers, and shells were individually numbered with non-toxic, waterproof ink. Whole prey mass (nearest 0.01 g) was determined for each prey item using an electronic scale. Several prey items of shell lengths ranging from 2.0 to 5.0 cm were placed on the platform at a time, and feeding behaviours exhibited by crows from the time of selection of a prey item from the platform to the end of consumption were observed and verbally recorded on a tape recorder. During this phase of the study, we only presented one prey species on each sample day, and observations were made until the crows stopped feeding at the platform, usually within 1 h. Using a stopwatch for timing, we then played back the recorded observations to determine the total amount of time individual birds spent flying, standing, and walking while consuming prey items. We only determined handling time for prey items that were dropped and consumed; prey items that were cached were not included in the analysis. In addition, as juvenile northwestern crows have been shown to be less efficient foragers (Richardson & Verbeek 1987), handling time observations for birds that could be visually identified as juveniles were excluded from this analysis.

We converted handling time measurements for individual prey items into energetic costs using the values reported by Zach (1979) for northwestern crows for flight (32.02 J/s), walking (10.67 J/s) and standing (7.12 J/s). Total energetic costs for handling prey (E_{cost}) were then determined by summing energetic costs of all foraging activities. To determine gross energy yield ($E_{\text{gross yield}}$) from mollusc shell size, we first converted shell length measurements for those prey items used in assessing handling time into dry tissue weight estimates using the following equations: *T. philippinarum* dry weight (dw) = $0.016 L^{3.47}$ (Richardson & Verbeek 1986); *N. lamellosa* dw = $2.09 L^{1.811}$, where L = shell length in mm (Menge 1972). Gross energy yield of each prey item was then determined using a conversion value of 20.0 kJ/g dw for littleneck clams (Richardson & Verbeek 1986), and 20.846 kJ/g dw for whelks (Menge 1972), and we determined net energy gain (E_{net}) by subtracting E_{cost} from the $E_{\text{gross yield}}$ of that item. Rate of energy gain (profitability) for crows feeding on individual prey items was then calculated by dividing E_{net} by the total time (s) that a crow spent handling that prey.

For each prey species, we used regression analysis with rate of energy gain (profitability) plotted against whole mass to generate standard curves, which we used to predict profitability of prey items in subsequent prey preference trials.

Prey Preference Trials

To test the hypothesis that crows feeding on hard-shelled molluscs apply a general decision rule based on prey mass, we provided crows with equal numbers of clams and whelks (15 of each species) on the feeding platform, without replacement, and recorded the items selected by crows over 1 h. We

used three prey species comparisons where clams and whelks differed both in profitability and mass. Comparisons included: (1) clam length 2.0–2.9 cm paired with whelks 4.0–4.9 cm, referred to hereafter as ‘small clams’ and ‘large whelks’; (2) clams 2.0–2.9 cm with whelks 3.0–3.9 cm, (‘small clams’ and ‘medium whelks’); and (3) clams 4.0–4.9 cm with whelks 4.0–4.9 cm (‘large clams’ and ‘large whelks’). We used two-sample t-tests to analyze differences in clam and whelk mass and profitability for each prey species combination. Based on differences in prey mass, we predicted that crows would select whelks in combinations 1 and 2, and clams in combination 3, despite the greater profitability of clams across all prey combinations (see Results). We tested one combination per day, and varied the order of presentation of prey size combinations between sample days, for a total of four trials per prey combination. If all of one species had been selected from the platform before 1 h had elapsed, we ended trials at that point to ensure that crows always had a choice of both prey species. Heterogeneity tests were applied to the four trials in each prey combination to ensure crows responded uniformly prior to pooling results, and we then assessed pooled data with chi-square goodness-of-fit tests to determine if crows selected prey items non-randomly in each combination. As we did not replace prey items that were selected during a trial, however, the clam:whelk availability ratio shifted as crows removed preferred items. To ensure the observed preferences of crows were uniform throughout each trial despite changes in the relative availability of clams and whelks, we used heterogeneity tests to compare the proportions of each prey type selected during the first half of all trials to those selected during the second half, for each prey combination. Analyses were performed using spss 11.0, with a significance level of 0.05. Means are presented as ± 1 standard error.

Results

For crows feeding on whelks, whole mass (M , in g) of whelks was linearly related to profitability (P , in J/s) according to the function $P = 7.31(M) + 148.55$ ($F_{1,14} = 6.68$, $P = 0.02$). To generate a standard curve for predicting profitability from whole mass of clams, we first square root transformed the profitability values calculated from handling time data; this variable was linearly related to whole mass of clams (M , in g) according to the function $P = 1.35(M) + 9.40$ ($F_{1,40} = 500.68$, $P < 0.001$). For all combinations used in prey preference trials, both the average mass and profitability differed between prey species (Table 1). Whelks were heavier than clams in combinations 1 and 2, while clams were heavier than whelks in combination 3; across all combinations tested, clams were more profitable than whelks.

For each prey combination, responses of crows across trials were uniform (heterogeneity test, combination 1: $\chi^2 = 2.25$, d.f. = 3, $P > 0.50$; combination 2: $\chi^2 = 6.47$, d.f. = 3, $P > 0.05$; combination 3: $\chi^2 = 5.21$, d.f. = 3, $P > 0.10$). Thus, subsequent analyses for each combination were performed on pooled data. In prey combination 1, where small clams were presented with large whelks, crows

Table 1: Mass and profitability of prey types [$\bar{x}(\pm SE)$], and statistical test results for three combinations of prey types presented to northwestern crows. Net energy gain and mean handling time for each prey type (estimated from handling trials) are also provided. See Methods for an explanation of prey size ranges in each combination.

	Prey combination	Mass (g)	Net E gain (kJ)	Handling time (s)	Profitability (J/s)
1	Small clams	5.8 ± 0.3	18.7 ± 6.3	83.1 ± 20.6	306.6 ± 13.4
	Large whelks	16.1 ± 0.3	37.1 ± 4.0	134.8 ± 37.8	266.4 ± 2.5
	t-Test	t = 23.16, d.f. = 115, P < 0.001			t = 2.96, d.f. = 63, P = 0.004
2	Small clams	6.3 ± 0.3	18.7 ± 6.3	83.1 ± 20.6	328.8 ± 12.9
	Medium whelks	8.3 ± 0.4	25.1 ± 4.8	126.4 ± 15.2	209.4 ± 2.9
	t-Test	t = 4.179, d.f. = 105, P < 0.001			t = 9.07, d.f. = 65, P < 0.001
3	Large clams	25.5 ± 0.7	187.9 ± 24.6	61.4 ± 18.6	1964.4 ± 80.2
	Large whelks	15.8 ± 0.3	37.1 ± 4.0	134.8 ± 37.8	263.7 ± 2.1
	t-Test	t = 13.41, d.f. = 80, P < 0.001			t = 21.20, d.f. = 59, P < 0.001

selected whelks almost exclusively over clams (59 of 63 items selected: $\chi^2 = 97.44$, d.f. = 1, $P < 0.001$). When we provided a combination of small clams and medium whelks, crows also showed a preference for whelks (56 of 78 items selected: $\chi^2 = 39.89$, d.f. = 1, $P < 0.001$), though this preference was less pronounced. However, when large clams were paired with large whelks in combination 3, crows switched to selecting mostly clams (55 of 74 items selected: $\chi^2 = 43.18$, d.f. = 1, $P < 0.001$) (Fig. 1). These observed preferences were consistent throughout each trial: for each prey combination, crow preferences during the first half of trials did not differ from preferences during the second half (heterogeneity tests, all P 's ns).

Discussion

When presented with clams and whelks differing in mass and profitability, crows showed strong preferences for heavier prey items, even where those items were the less profitable option (Fig. 1). These results support the hypothesis that crows apply common decision rules across prey species requiring similar handling methods. Implicit in this is the assumption that crows are able to categorize prey types according to biologically relevant criteria; this ability has been demonstrated in other birds (e.g. Pepperberg 1987), including other corvids (e.g. Real et al. 1984), and it is therefore not unreasonable to expect a similar cognitive capacity in northwestern crows. In at least some parts of their

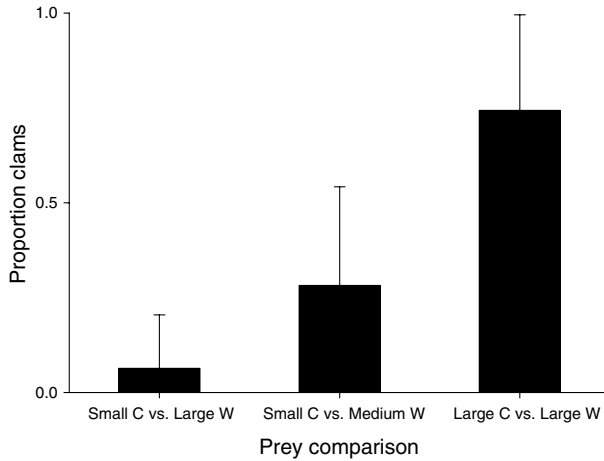


Fig. 1. Number of clams selected by northwestern crows as a proportion of total prey items selected (C, clams or W, whelks) when three different prey species size combinations were presented. For each combination, data represent the pooled results of four trials. Total number of prey items selected in comparison 1: $n = 63$, comparison 2: $n = 78$, comparison 3: $n = 74$. See methods for a description of prey size ranges in each comparison

range, juvenile northwestern crows are reported to experience high mortality because of starvation (Richardson et al. 1985), suggesting strong selective pressure for rapid acquisition of foraging skills. This may best be achieved by learning general decision rules that apply to a wide range of prey types, such as those encountered in variable intertidal environments (e.g. Wootton 1997). Crows visiting the feeding platform were frequently observed to pick up and replace several items, as though assessing mass, before making a selection. While previous studies have shown that birds feeding on a single prey type appear to assess prey mass and select heavier items (e.g. Heinrich et al. 1997; Langen & Gibson 1998), this is to our knowledge the first study that demonstrates a similar behaviour applied across prey types.

Theory suggests that, although the payoff resulting from decisions based on simple rules is always less than that resulting from optimal models, the magnitude of the difference between these payoffs tends to be minimal (Janetos & Cole 1981). In this study, crows selected whelks over clams in combinations 1 and 2, where clams would have yielded an additional 40 and 119 J/s, respectively, more than whelks. However, when large clams were paired with large whelks in combination 3, crows selected more clams, gaining an average payoff of 1700 J/s greater than that yielded by whelks (Table 1). Thus, results of this study support the suggestion that decision rules approximate optimal solutions (Janetos & Cole 1981), as crows selecting heavier molluscs only made suboptimal choices when the difference in profitability between prey types was relatively small.

The ability of avian predators to distinguish between similar prey types was demonstrated in American crows (*Corvus brachyrhynchos*) feeding on two species

of walnut that differed in energetic yield and handling time (Cristol 2001). When crows were presented with a choice between one walnut of each species, both of approximately the same mass, they consistently selected the species providing the greatest energy yield (Cristol 2001). It is noteworthy, however, that this preference was apparent when birds were presented with walnuts of the same mass; it is probable that under natural foraging conditions, a decision rule leading them to select the heaviest item would be applied by crows feeding on walnuts, regardless of the species or associated profitability. Thus, it may be more important to identify decision rules generating preferences under more complex choice conditions to accurately predict prey preferences, and to understand the potential impact of generalist avian predators on prey populations (e.g. Whoriskey & Fitzgerald 1985; Wootton 1997).

When crows are presented with more than one prey type, prey mass may serve as a reliable predictor of an energetic currency other than profitability, such as net energy gain (Table 1). Predators simultaneously encountering multiple prey items are predicted to maximize net energy gain rather than profitability when prey encounter rates are low (Stephens & Krebs 1986). However, in this study prey encounter rates were likely to have been perceived by crows as relatively high, as prey items were supplied on the platform in high densities, clams and whelks are naturally abundant around the study area, and alternative food sources for crows in the surrounding urban environment are readily available. Thus, under these experimental conditions, the optimal foraging solution should maximize profitability rather than net energy gain (Stephens & Krebs 1986).

Comparisons of energetic differences between prey species often ignore important differences in other currencies such as nutrient content, which may have significant effects on predator foraging decisions (Stephens & Krebs 1986). Reproductive output of birds is known to be limited by calcium availability (Tilgard et al. 2002), and birds such as corvids frequently consume eggshells or mollusc shells when these items are encountered in the environment (Dhondt & Hochachka 2001). During development, juvenile crows seem particularly vulnerable to metabolic bone disease, a disorder that has been linked to diets low in bioavailable calcium (Tangredi & Krook 1999). Thus, there should be strong selective pressure for maximizing calcium intake, and prey preferences of crows may therefore reflect differences in calcium content or availability among prey types. Acid solubility of bivalve shell is reported to be considerably higher than gastropod shell (87% vs. 45%, respectively; Ajakaiye et al. 1997) and, given that mollusc shells are also frequently consumed (pers. obs.), crows may therefore obtain more dietary calcium when feeding on clams. Alternatively, prey selection might be affected by differences in total energy stored as lipids; lipids comprise 18–19% of the body mass of whelks (Stickle & Duerr 1970), but only 1% in clams (R. Reid, pers. comm.). Thus, lipid intake of crows feeding on whelks would be greater than when feeding on clams. If crows were limited by either calcium or lipids, they would be expected to preferentially select the prey species providing the greatest amount of this limiting resource. However, neither of these arguments

provides a consistent explanation for the prey preferences of crows in this study, as preferences shifted depending on the characteristics of the alternative prey presented.

This study provides evidence for the application of a general decision rule by crows feeding on two different prey types, and suggests that avian predators categorize prey according to similarities in handling methods. Categorization and the use of decision rules by dietary generalists may have several advantages. First, it may enhance the efficiency of foraging decisions by reducing the time needed to assess prey (Dukas & Waser 1994), which may in turn reduce the amount of time the forager is exposed to predation (Krause & Godin 1996), or at risk of food loss by kleptoparasitism by conspecifics (Ha & Ha 2003) or other species (Ens et al. 1990). Second, general decision rules can be applied to novel prey types that are classified by a predator as belonging to pre-existing categories (Dukas & Waser 1994), and skills learned while handling similar food types may be transferred to novel prey (Hughes & O'Brien 2001). For example, the English walnut (*Juglans regia*) has been introduced in the study area, and northwestern crows regularly drop walnuts on hard surfaces to break them open (pers. obs.). This prey dropping behaviour is used by crows feeding on hard-shelled molluscs and acorns (*Quercus garryana*) that occur naturally in the study area, but has since been applied to walnuts, as a novel prey item. While this suggests that crows categorize molluscs and nuts together as hard-shelled prey and apply a similar handling method, it is not known whether a common decision rule leading them to select the heaviest item would be applied by crows feeding on any combination of these food types. Studies of invertebrates have shown that preferences learned in one foraging situation do not transfer to novel situations that are sufficiently different (Blarer et al. 2002); however, the extent to which vertebrate predators are able to generalize across prey types and foraging situations requires further study. Given that northwestern crows forage both in terrestrial and marine intertidal habitats (Butler 1974), shifts in their prey preferences in response to changes in prey characteristics or abundance in one habitat may have potentially far-reaching effects.

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Literature Cited

- Ajakaiye, A., Atteh, J. O. & Leeson, S. 1997: Effects of calcium source, particle size and time on in-vitro calcium solubility of some indigenous Nigerian mineral ingredients for poultry diets. *Anim. Feed Sci. Tech.* **65**, 293—298.
- Bouskila, A. & Blumstein, D. T. 1992: Rules of thumb for predation hazard assessment: predictions from a dynamic model. *Am. Nat.* **139**, 161—176.

- Blarer, A., Keasar, T. & Scmda, A. 2002: Possible mechanism for the formation of flower size preferences by foraging bumblebees. *Ethology* **108**, 341—351.
- Butler, R. W. 1974: The feeding ecology of the Northwestern Crow on Mitlenatch Island, British Columbia. *Can. Field Nat.* **88**, 313—316.
- Cristol, D. A. 2001: American crows cache less preferred walnuts. *Anim. Behav.* **62**, 331—336.
- Dhondt, A. A. & Hochachka, W. M. 2001: Variations in calcium use by birds during the breeding season. *Condor* **103**, 592—598.
- Dukas, R. & Waser, N. M. 1994: Categorization of food types enhances foraging performance of bumblebees. *Anim. Behav.* **48**, 1001—1006.
- Ens, B. J., Esseling, P. & Zwarts, L. 1990: Kleptoparasitism as a problem of prey choice: a study of mudflat-feeding curlews, *Numenius arquata*. *Anim. Behav.* **39**, 219—230.
- Ha, R. B., & Ha, J. C. 2003: Effects of ecology and prey characteristics on the use of alternative social foraging tactics of crows, *Corvus caurinus*. *Anim. Behav.* **66**, 309—316.
- Heinrich, B., Joerg, C. C., Madden, S. S. & Sanders Jr, E. W. 1997: Black-capped chickadees and red-breasted nuthatches 'weigh' sunflower seeds. *Auk* **114**, 298—299.
- Hughes, R. N. & O'Brien, N. 2001: Shore crabs are able to transfer learned handling skills to novel prey. *Anim. Behav.* **61**, 711—714.
- Janetos, A. C. & Cole, B.J. 1981: Imperfectly optimal animals. *Behav. Ecol. Sociobiol.* **9**, 203—209.
- Krause, J. & Godin, J.-G. J. 1996: Influence of prey foraging posture on flight behaviour and predation risk – predators take advantage of unwary prey. *Behav. Ecol.* **7**, 264—271.
- Langen, T. A. & Gibson, R. M. 1998: Sampling and information acquisition by western scrub-jays, *Aphelocoma californica*. *Anim. Behav.* **55**, 1245—1254.
- Menge, B. A. 1972: Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monog.* **42**, 25—50.
- Micheli, F. 1995: Behavioural plasticity in prey-size selectivity of the blue crab *Callinectes sapidus* feeding on bivalve prey. *J. Anim. Ecol.* **64**, 63—74.
- Mitchell, W. A. 1989: Informational constraints on optimally foraging hummingbirds. *Oikos* **55**, 145—154.
- Pepperberg, I. M. 1987: Acquisition of same/different concept by an African gray parrot (*Psittacus erithacus*); learning with respect to categories of color, shape and material. *Anim. Learn. Behav.* **15**, 423—432.
- Real, P. G., Iannazzi, R., Kamil, A. C. & Heinrich, B. 1984: Discrimination and generalization of leaf damage by blue jays (*Cyanocitta cristata*). *Anim. Learn. Behav.* **12**, 202—208.
- Richardson, H. & Verbeek, N. A. M. 1986: Diet selection and optimization by northwestern crows on Japanese littleneck clams. *Ecology* **67**, 1219—1226.
- Richardson, H. & Verbeek, N. A. M. 1987: Diet selection by yearling northwestern crows (*Corvus caurinus*) feeding on littleneck clams (*Venerupis japonica*). *Auk* **104**, 263—269.
- Richardson, H., Verbeek, N. A. M. & Butler, R. W. 1985: Breeding success and the question of clutch size of northwestern crows *Corvus caurinus*. *Ibis* **127**, 174—183.
- Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton Univ. Press, Princeton, NJ, USA.
- Stickle W. B. & Duerr, F. G. 1970: The effects of starvation on the respiration and major nutrient stores of *Thais lamellosa*. *Comp. Biochem. Physiol.* **33**, 689—695.
- Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S. E. A. le V. dit, Caldow, R. W. G., McGroarty, S. & Clarke, R. T. 2000: Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *J. Appl. Ecol.* **37**, 564—588.
- Tangredi, B. P. & Krook, L. P. 1999: Critical secondary hyperparathyroidism in free-living fledgling American crows (*Corvus brachyrhynchos brachyrhynchos*). *J. Zool. Wildlife Med.* **94**, 94—99.
- Tilgard, V., Mänd, R. & Mägi, M. 2002: Calcium shortage as a constraint on reproduction in great tits *Parus major*: a field experiment. *J. Avian Biol.* **33**, 407—413.
- Verbeek, N. A. M. & Butler, R. W. 1999: Northwestern crow (*Corvus caurinus*). In: *The Birds of North America* (Poole, A. & Gill, F., eds). The Birds of North America, Inc., Philadelphia, PA, USA. pp. 407.
- Whoriskey, F. G. & Fitzgerald, G. J. 1985: The effects of bird predation on an estuarine stickleback (Piscea: Gasterosteidae) community. *Can. J. Zool.* **63**, 301—307.

- Wootton, J. T. 1997: Estimates and tests of per capita interaction strength: diet, abundance, and impact of inter-tidal foraging birds. *Ecol. Methods* **67**, 45—64.
- Zach, R. 1979: Shell dropping: decision making and optimal foraging in northwestern crows. *Behaviour* **68**, 106—117.

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