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## Fear and Food Recognition in Naive Common Ravens

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One of the major problems an animal experiences upon reaching independence is recognizing enemies and appropriate food. Numerous studies show that specific reactions to stimuli associated with food or danger may be found in naive predators (e.g. Smith 1975, Caldwell and Rubinoff 1983, Schuler and Hesse 1985, Roper 1990). However, they may be modified with experience. For example, recognition of broad categories such as a specific color is a first filter that narrows the range of possibilities of what is acceptable, and learning then refines the specifics (Coppinger 1969, Roper 1990).

Common Ravens (*Corvus corax*) are of special interest for studies of food recognition because they are both generalist feeders and carcass specialists for at least part of the year (Bent 1946). As generalist feeders living in a wide range of habitats, they approach (and "test") a great variety of potential food items (Heinrich 1995) and, as carcass specialists, they also are predictably attracted to dead animals (Heinrich 1988a). However, reposing large animals can be dangerous to approach and we predicted, therefore, that such large potential food objects would be attractive, but approached only with great caution. Here we examine the ontogeny of feeding preferences in hand-reared birds of known experience in order to determine whether naive young ravens are attracted and/or fearful of specific stimuli associated with potential food.

**Methods.**—We removed 10- to 15-day-old fledgling common Ravens from five nests and maintained them in five separate sibling groups housed in large, outdoor aviaries (40–60 m<sup>3</sup>). All young were fed small pieces of meat, dog food, and commercial chicken starter.

We presented a variety of test items to the young for up to nine months after fledging. Test items were presented to the birds after they were held one day without food and, during the test, they were not given alternative food. (Although ravens readily eat decaying meat, we provided only fresh carcasses.) If the test item was edible, the ravens were allowed to consume it (or at least part of it) before the next item was presented. All of the large mammals that were presented as test items were relatively intact, but were usually cut open so as to reveal meat. Prior to testing, the young ravens had not been exposed to whole-animal carcasses, nor to any of the items subsequently used during testing.

In one subgroup of five birds, interactions with

people during test feeding were kept to a minimum. The observer placed test objects in the cage, then watched from a small window in a nearby structure. In another of the subgroups of three birds, the observer again dumped food into the cage, then observed the birds through a picture window. In the third to fifth groups of three, two, and four birds, respectively, the observers stayed next to the birds, but outside the wire cage during the feeding trials.

Dominance was one of the variables affecting access to food. Birds in each group established a linear dominance hierarchy soon after fledging. Dominance was scored at encounters over food (see Marzluff and Heinrich 1991), with a bird yielding to a threat by another being scored as subordinate to it. Reversals in hierarchies were rare, and we ranked members of each group in the order that minimized these reversals.

**Results.**—Ravens varied dramatically in the time to first contact of different novel items, food and otherwise. Ravens of all five groups almost immediately approached all round, smooth objects. For example, average lengths of time to contact were: (1) 29 s for plastic "eggs," chicken eggs (white, brown, green and red), and Ostrich (*Struthio camelus*) eggs; (2) 122 s for vegetables and fruits (red and green tomatoes, potatoes, lettuce core, red chiles, green pepper, yellow and red apples, orange pumpkin); and (3) 2.5 s for inanimate round objects (blue ball, ball of aluminum foil, golf ball, balloon; Table 1). There was no significant difference in the time to contact for these three types of items, and all were contacted significantly sooner than snakes, inanimate long objects, large mammals, and large birds (Table 2). These data indicate that, regardless of color and a large range of size, the naive birds are highly attracted to round and smooth objects.

Long and thin objects, in contrast, appeared to be ignored. They were usually contacted only after many hours and then without any apparent fear. Both garter snakes (*Thamnophis sirtalis*; 30–50 cm) and inanimate long objects (black hose and aluminum-foil rolls of lengths similar to those of the snakes) were contacted on average in 7.8 and 16 h (Table 1), respectively, but there was no significant difference in these times to contact (Table 2). Approach to these objects was significantly slower than approach to round objects mentioned above, or to mice, small birds, fish, and amphibians (Table 2). Similarly, the birds invariably attacked an aluminum-foil round ball almost "instant-

TABLE 1. Time (h) required for captive hungry Common Ravens to first contact different food types and other novel objects.

Type	n	$\bar{X} \pm SD$ (range)
Egg	5	0.008 $\pm$ 0.014 (0.0003-0.0330)
Vegetable and fruit	12	0.034 $\pm$ 0.063 (0.0003-0.1670)
Inanimate, round object	10	0.0007 $\pm$ 0.0070 (0.0003-0.0170)
Snake	4	7.75 $\pm$ 10.96 (0.01-24.00)
Inanimate, long object	3	16.00 $\pm$ 13.85 (0.013-24.00)
Large mammal	11	15.71 $\pm$ 16.63 (0.05-48.00)
Mouse	3	0.039 $\pm$ 0.042 (0.0003-0.0830)
Large bird	6	6.13 $\pm$ 13.17 (0.33-33.00)
Small bird	4	0.145 $\pm$ 0.237 (0.017-0.500)
Fish	4	0.02 $\pm$ 0.017 (0.0003-0.0360)
Amphibian	5	0.16 $\pm$ 0.128 (0.0003-0.2500)

ly" and then tore it to shreds, but the same aluminum foil made into an elongate shape was ignored for nearly a day and even then only haphazardly contacted and never torn apart. Naive Common Ravens, therefore, are not repelled by long objects, but they also are not attracted to them.

Carcasses of large mammals (raccoons [*Procyon*], domestic cats [*Felis*], skunks [*Mephitis*], porcupines [*Erethion*], rabbits [*Sylvilagus*] and hares [*Lepus*], squirrels [*Sciurus*], woodchucks [*Marmota*]) and large birds (Ruffed Grouse [*Bonasa umbellus*], Mallard [*Anas platyrhynchos*], Common Raven) placed in the ravens' aviaries for the first time elicited immediate alarm in all five groups of ravens. The birds often bounced against the wire screening, made alarm calls, and/or hid in their roosting sheds. After several hours and/or days, the ravens typically approached the animal repeatedly. At each new approach they came closer, until one bird touched the dead animal, and jumped back. Dead animals almost invariably were approached and touched on the tail first. In some cases much of the hair was removed from the tail of a dead mammal as the birds made repeated yanks before they investigated further. After repeated contacts of the carcass, the ravens became bolder and then soon fed on the exposed meat of the animal. Large mammals and large birds were approached significantly slower than all

objects except snakes and inanimate, long objects (Table 2).

Unlike large mammals and birds, small ones were approached almost immediately, with an average of 2.3 min for song birds and 8.7 min for mice (Table 1). There was no significant difference in approach time between that for smooth, round objects and small birds or mice (Table 2). However, small birds and mice were approached significantly sooner than long objects, large mammals, and large birds (Table 2). Fish and amphibians were approached quickly.

Ravens learned not to fear all types of food items. More rapid approach was seen at almost all items after one or two encounters (Fig. 1). Even mice and chicken eggs, which were accepted almost "immediately" (within 2 to 3 min) were uniformly approached within 5 to 10 s after the second or third encounter (Fig. 1). Similarly, raccoons (which were feared and not contacted in the first 24 h) were contacted in less than 2 h during trials subsequent to the first. Although the ravens accepted small birds immediately, the ravens exhibited a variable response to large ones (grouse and ducks). Initial contact (except with the dead raven) to large birds required considerably less than 24 h, but even after the fourth encounter there was still a delay of over an hour in one group of birds.

Do the birds get less shy of all strange items with

TABLE 2. Comparisons between time to first contact for different food types (results of one-way ANOVAs).

Item	1	2	3	4	5	6	7	8	9	10
1 Egg										
2 Vegetable and fruit	ns									
3 Inanimate round object	ns	ns								
4 Snake	*	*	*							
5 Inanimate long object	*	*	*	ns						
6 Large mammal	*	*	*	ns	ns					
7 Mouse	ns	ns	ns	*	*	*				
8 Large bird	*	*	*	ns	ns	ns	*			
9 Small bird	ns	ns	ns	*	*	*	ns	*		
10 Fish	ns	ns	*	*	*	*	ns	*	ns	
11 Amphibian	ns	ns	*	*	*	*	ns	*	ns	ns

\*,  $P < 0.05$ ; ns,  $P > 0.05$ .

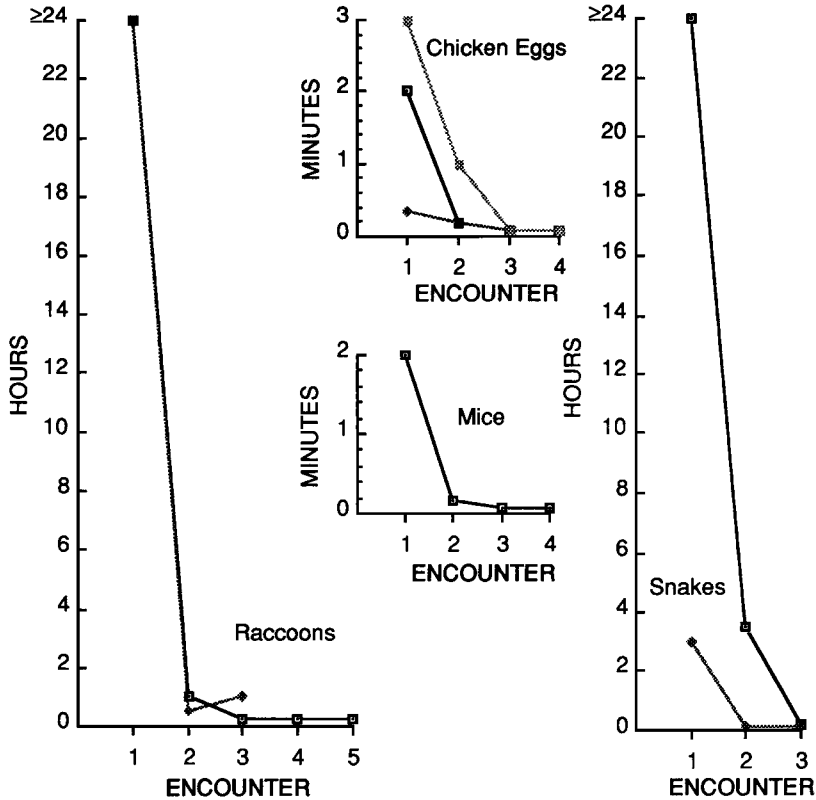


Fig. 1. Time until first contact (as function of number of encounters) at chicken eggs, mice, raccoons, and garter snakes. Three groups of birds tested: (1) square symbols with centered dots indicate results for group of three birds; (2) shaded squares for a second group of three birds; and (3) shaded diamonds for group of five birds.

experience and/or age, or do they learn not to be shy of specific items? To help answer this question we examined time to contact as a function of absolute time each experiment was conducted (mid-August 1989 to February 1990). The results were ambiguous. With one group of five birds during the first three encounters with large animals (a gray squirrel [*Sciurus carolinensis*], a woodchuck, and a raccoon), contact did not take place within the first day. However, subsequent contacts with these animals occurred in an hour or less, even when these animals were presented as much as 20 days later. However, previously unencountered animals (domestic cat, porcupine, hare, and calf) were contacted less than 1 h after the first three respective encounters. In contrast, the results of another group (three ravens) showed that all large animals are not treated uniformly as one class, and that learning not to fear one type does not necessarily transfer to another type. For example, although raccoons were quickly approached on all five encounters after the first time, a porcupine, a deer (*Odocoileus*), and a white domestic cat were not contacted for 20, 44 and 18 h, respectively, when first encountered,

even though for over a month raccoons had always been contacted in less than 15 min.

First contact at all types of food was dependent on dominance (one-way goodness-of-fit test comparing numbers of approaches by status,  $X^2 = 83.3, P < 0.001$ ). However, there was a difference between feared food (where birds showed escape reactions) and food contacted within 5 min. At the latter, the  $\alpha$  bird (i.e. dominant) was almost four times more likely than any of the other birds to make first contact and to feed and exclude the others (Table 3). At feared food, however,  $\alpha$  birds were less likely to first contact food than at food that was not feared (i.e. approached with little hesitation; two-way test of independence comparing numbers of approaches by status to feared and "unfeared" foods,  $X^2 = 15.3, df = 2, P < 0.001$ ).

*Discussion.*—Birds have recognition patterns for potential enemies (e.g. harmful snakes; Smith 1975), nest sites (Marzluff 1988), suitable habitat (James 1971), and food (Roper 1990). However, learning can presumably modify their responses.

Common Ravens in the wild use a great variety of food (for review, see Heinrich 1989), and food taken

varies with raven age and/or season. In northern Minnesota, the immature nomadic birds feed heavily on carcasses in the winter, while the adult resident birds feed more on small mammals and birds, possibly secured by hunting (Bruggers 1988). In the summer, both groups feed on fruits, but rarely on snakes and amphibians. For a food generalist one would predict that a large animal carcass would be more an object to fear than an object to be approached for a meal.

Our primary results confirm and extend previous observations that inexperienced Common Ravens have perhaps an exaggerated neophobia (Gwinner 1964), particularly at large animal carcasses. However, the neophobia is not as general as had been supposed (Heinrich 1988b). We show here that naive birds are attracted to new objects, provided they are round and smooth. However, the young ravens are indifferent to long thin objects that the birds have never before encountered.

In nature, there are few round and smooth objects except eggs, fruits, and possibly rocks. Eggs and fruits are common food items for Common Ravens in the summer (Stiehl 1978, Bruggers 1988). Thus, to immediately approach round, smooth objects should on the average be profitable, since eggs were one of the ravens' favorite foods. Long, thin objects are apt to be branches, and given that branches far outnumber snakes, it might on the average be counterproductive for a naive raven to stop and investigate every immobile, long object.

Aside from possible movement (which we did not investigate), a third major and general feature that the naive ravens recognized was hair/feather covering (i.e. fuzziness). As indicated previously (Heinrich 1989), some naive ravens immediately approached, picked up, and ate smooth caterpillars. However, fuzzy ones were treated with caution; young juvenile ravens confronting a fuzzy caterpillar did the neophobic "jumping-jack" maneuvers, only gradually drawing closer.

The fourth major feature that affected the ravens' behavior was prey size. In general, the larger the potential food object, the more hesitantly it was approached. (We use size in a loose sense here, in that although individual items such as mussels, prawns, pieces of bread, or meat were immediately approached, piles of them were sometimes left untouched for hours by all five groups of birds). The tension between attraction and repulsion of carcasses was resolved by learning. By repeated trial approaches the birds gradually learned to lose their caution at any one specific kind of carcass.

Ideally, ravens should perhaps have recognition of features that distinguish between live and dead animals. Obviously, the first is movement, and we presume the birds routinely avoid large, live animals because of movement, in the same way they are presumably attracted to very small ones because the latter move. Another potentially obvious recognition fea-

TABLE 3. Effect of status on first contact of food at unfeared food (contacted within 5 min) and feared food (contacted after 5 min or more) in two kin groups of three birds each. Numbers indicate separate instances of first contact by respective birds.

	Dominance position <sup>a</sup>			Total
	$\alpha$	$\beta$	$\gamma$	
Not feared	108	27	18	153
Feared	26	18	17	61
Total	134	45	35	214

<sup>a</sup>  $\alpha$ ,  $\beta$ , and  $\gamma$  refers to position in dominance hierarchy, with  $\alpha$  being the most dominant bird.

ture that could identify a large, furry object as potential food is visible meat or blood. However, one of our primary conclusions is that this does not suffice; large carcasses routinely had blood/meat visible, but were still actively avoided. Note that recognition of meat as food could be learned in the nest.

In previous studies with captive Common Ravens (Gwinner 1964, Heinrich 1989), the most dominant birds were the leaders or "initiators" in contacting strange food items. We here confirm these observations. Why do the dominants go first? Heinrich (1989) suggested it may be related to sexual selection, with dominant males attempting to demonstrate their potential ability as a food provider. Our present results in the context of the current study do little to support this hypothesis. Our dominant birds made no effort to be first at feared food (where it might have paid to "show off"). They were, instead, first at unfeared food. Presumably, even if our dominant birds had dared to be first to approach feared food, they could not have demonstrated their dominance because they might not have been contested. However, perhaps they feared the food and, knowing they could quickly displace the subordinates, they waited for a subordinate to make the first move to see if the food was safe. Our results do not distinguish between these two possibilities. Social interaction at food is obviously important, but it is as yet little understood.

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#### LITERATURE CITED

- BENT, A. C. 1946. Life histories of North American jays, crows and titmice. U.S. Natl. Mus. Bull. 191.  
BRUGGERS, D. J. 1988. The behavior and ecology of the Common Raven in northeastern Minnesota.

- Ph.D. dissertation, Univ. Minnesota, Minneapolis.
- CALDWELL, G. S., AND R. W. RUBINOFF. 1983. Avoidance of venomous sea snakes by naive herons and egrets. *Auk* 100:195-198.
- COPPINGER, R. P. 1969. The effect of experience and novelty on feeding behavior with reference to the evolution of warning coloration in butterflies. I. Reactions of wild-caught adult Blue Jays to novel insects. *Behaviour* 35:45-60.
- GWINNER, E. 1964. Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkraben (*Corvus corax* L.). *Z. Tierpsychol.* 21:657-748.
- HEINRICH, B. 1988a. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. *Behav. Ecol. Sociobiol.* 23:141-156.
- HEINRICH, B. 1988b. Why do ravens fear their food? *Condor* 90:950-952.
- HEINRICH, B. 1989. Ravens in winter. Summit Books of Simon & Schuster, New York.
- HEINRICH, B. 1995. Neophilia and exploration in juvenile Common Ravens, *Corvus corax*. *Anim. Behav.* 50:695-704.
- JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-235.
- MARZLUFF, J. 1988. Do Pinyon Jays alter nest placement based on prior experience? *Anim. Behav.* 36:1-10.
- MARZLUFF, J., AND B. HEINRICH. 1991. Foraging by Common Ravens in the presence and absence of territory holders: An experimental analysis of social foraging. *Anim. Behav.* 42:755-770.
- ROPER, T. J. 1990. Responses of domestic chicks to artificially coloured insect prey: Effects of previous experience and background colour. *Anim. Behav.* 39:466-473.
- SCHULER, W., AND E. HESSE. 1985. On the function of warning coloration: A black and yellow pattern inhibits prey-attack by naive domestic chicks. *Behav. Ecol. Sociobiol.* 16:249-255.
- SMITH, S. M. 1975. Innate recognition of coral snake pattern by a possible avian predator. *Science* 187:759-760.
- STIEHL, R. B. 1978. Aspects of the ecology of the Common Raven in Harney Basin, Oregon. Ph.D. dissertation, Portland State Univ., Portland, Oregon.

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## Survival Rates of Puerto Rican Birds: Are Islands Really That Different?

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The comparison of tropical birds having small clutches and long lifespans with temperate birds having large clutches and short lifespans is one of the cornerstones of theories dealing with avian reproductive strategies (Cody 1966, 1971, Stearns 1976, Ricklefs 1983, 1992, Murray 1985, Skutch 1985, Godfray et al. 1991). Karr et al. (1990) described the limited data supporting the assumption of long tropical lifespans and provided data for one sample of tropical birds—25 species from Panama—that did not show greater survivorship than a sample of temperate species (10 from Maryland). Their paper provides one of the first comparisons of long-term data from sets of species from two regions with survival rate estimates computed using capture-recapture models developed in recent years to permit inferences unconfounded by sampling probabilities (Pollock et al. 1990).

To better understand whether regional differences

in avian survival rates occur, more mark-recapture data are needed for analysis using the above models. Here, we offer a long-term data set on the survivorship of 12 species of Puerto Rican birds computed with the models used by Karr et al. (1990). We compare these data and other known demographic traits of resident Puerto Rican species living in a dry-forest community with those of Karr et al. (1990) for Panama and Maryland, and suggest how the Puerto Rico data comply with common assumptions about tropical birds. We recognize that only with the accumulation of many such data sets from all areas can one confidently generalize about the demographic traits upon which so many evolutionary models rest.

*Study area and methods.*—Our studies were done within the Guanica State Forest in southwestern Puerto Rico. This 4,000-ha tract of subtropical deciduous forest has been protected by the Commonwealth of