

Kinship and Association in Social Foraging Northwestern Crows (*Corvus caurinus*)

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The producer–scrounger model suggests that the number of producers (animals that search for food) and scroungers (animals that consume food found by producers) may be an evolutionarily stable strategy. We investigated the role of kinship and social affiliation on these strategies by combining microsatellite DNA-based measures of relatedness with focal animal behavioral sampling of northwestern crows in the field. Scrounges were either passive (quiet ground approach without pursuit) or aggressive (noisy approach with pursuit). The combination of individually marked animals and information on relatedness allowed investigation of the roles of dominance and kinship in scrounging, including the target and form of the scrounge. Crows in foraging groups were more likely to be associated (i.e., socially affiliated) than were birds in the background population, but were not more likely to be genetically related than were birds in the background population. There was no difference between the average association of the foraging group and the average association between the scrounge interactors. There was also no difference in the average association between passive and aggressive scrounge interactions. Adults were more likely than juveniles to demonstrate a preference for social companions, and males were more likely than females to demonstrate a preference for social companions. Within foraging groups, passive scrounges tended to occur between more closely related individuals, and aggressive scrounges among less closely related individuals. Thus, scroungers modulate their mode of scrounging according to relatedness, or producers modulate their response, or both. They discriminate close from more distant relatives or unrelated individuals by adjusting the level of aggressiveness associated with theft.

Association Producer Relatedness Scrounger

The evolutionarily stable strategy (ESS) concept was originally developed to explain aggressive encounters, but has been expanded to include all social interactions that are frequency dependent (Maynard Smith, 1974). Food-stealing behavior has been viewed as a producer–scrounger game, and we use the terminology of that literature here. The pro-

ducer–scrounger (PS) model suggests that the number of producers (animals that search for food) and scroungers (animals that consume food found by producers) may result from an ESS (Barnard & Sibly, 1981; Barta & Giraldeau, 2000; Beauchamp & Giraldeau, 1996; Giraldeau, Soos, & Beauchamp, 1994). Predicted proportions of producers and

scroungers are based on models where individuals maximize their net intake of food (Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991) or minimize their risk of starvation (Caraco & Giraldeau, 1991). Experimental tests of the models are recent (Beauchamp & Giraldeau, 1997; Giraldeau et al., 1994; Koops & Giraldeau, 1996; Lefebvre & Helder, 1997), although numerous studies have been done on kleptoparasitism or food piracy, both interspecific (Belisle, 1998; Brockmann & Barnard, 1979; Thompson, 1986) and intraspecific (Bautista, Alonso, & Alonso, 1998; Steele & Hockey, 1995).

Vickery et al. (1991) considered the effect of kinship on scrounging by suggesting that the absence of scrounging might occur through reciprocal or kin-selected altruism. Work with termites (Kaib, Hussender, Epplen, Epplen, & Brandl, 1996) and fish (Brown & Brown, 1996) indicates that foraging takes place in the company of kin, but does not address variation in foraging strategies by kinship. Indeed, this has rarely been addressed (Sklepkovych, 1997, but see Barkan, Craig, Strahl, Stewart, & Brown, 1986). However, Hatch and Lefebvre (1997) found that juvenile ringdoves foraged more often with related rather than with unrelated birds, but did not preferentially acquire social foraging information from kin. Sklepkovych (1997) found that adult Siberian jays discriminated between kin and nonkin while foraging, specifically by tolerating juvenile kin over juvenile nonkin at bait sites.

Perhaps scroungers are related to producers, and producers receive indirect fitness benefits for "allowing" scrounging. This is similar to Sklepkovych's (1997) finding that adults "tolerated" juveniles at feeding sites, particularly related juveniles. Alternatively, being scrounged upon may be an unavoidable cost to social foraging, and scroungers may therefore focus stealing on nonrelatives. This is supported by the vast literature on interspecific kleptoparasitism (see Belisle, 1998; Brockmann & Barnard, 1979; Thompson, 1986). Thus, there are reasonable explanations for each hypothesis. If scrounge interactions occur among unrelated interactors, then that would suggest that scrounging is potentially a cost to social foraging (but see Beauchamp, 2000; Ranta, Peuhkuri, Hirvonen, & Barnard, 1998). Alternatively, if scrounge interactions occur among related interactors, then this would be more consistent with a kin selection argument

(Hamilton, 1964). Here we show that individuals discriminate close from more distant relatives or unrelated individuals by adjusting the level of aggressiveness associated with the interaction.

Beach-foraging northwestern crows (*Corvus caurinus*) feed on intertidal invertebrates such as clams, worms, shore crabs, and snails (Robinette & Ha, 2000, 2001). In addition, they dig Pacific sand lances (*Ammodytes hexapterus*) out of the intertidal mud at low tides (see Robinette & Ha, 1997). These prey items are discrete and vary in their visibility to conspecific foragers. Small prey items are quickly consumed with short handling times, while larger prey items such as clams and fish require longer handling times and provide increased opportunities for other foragers to steal ("scrounge") from the finder or producer (Barnard & Sibly, 1981; Giraldeau et al., 1994; Robinette & Ha, in review). These intertidal prey are energetically valuable (Robinette & Ha, 1997) and social groups of birds from relatively distant locations converge on this beach during times of intertidal exposure. In wooded home locations, northwestern crows tend to be mildly territorial, defending an area around prime nest sites.

During observations, we noted that scrounges take two clearly discrete forms: one aggressive, and the other passive. During the aggressive encounters, individuals physically attack one another and engage in chasing and vocalizations. During a passive scrounge, an individual simply displaces another without engaging in conflict, chase, or vocalization. An initial impression suggests dominance as the cause, but the observation of juveniles displacing adults argues against that assumption (Robinette & Ha, unpublished). We question the degree to which our data reflect differential behavior towards relatives or simply differential behavior towards those animals with which scroungers are most familiar. Thus, we have measured association among groups of animals in our population. The results demonstrate the use of the association index to quantify the degree of affiliation, and thus familiarity, of various groups of animals. Indeed, this index provides pairwise measures of association parallel to the pairwise measures of kinship calculated from the DNA marker data. The combination of individually marked animals and information on relatedness allowed investigation of the roles of dominance, affiliation, and kinship in scrounging, including the target and form of the scrounge. We investigated the

role of kinship and social affiliation on foraging strategies in northwestern crows by combining microsatellite DNA-based measures of relatedness with focal animal behavioral sampling in the field.

Affiliation, or the tendency of individuals to consistently physically associate with specific other individuals, can be quantified using an association index. The use of association indices allows researchers to quantify and compare the strength or weakness of bonds between individuals and age/sex classes of animals within groups. There are several methods used to quantify association patterns, including the half-weight index (which uses an average of the number of sightings of the two individuals), the twice-weight index (which counts each observation as an independent event), and the simple index (considered by Ginsberg & Young, 1992, to be the most accurate).

According to Cairns and Schwager (1987), the half-weight index is the least biased of the indices if animals are more likely to be sighted when separate than when together. Ginsberg and Young (1992) suggested that this index tends to overestimate associations because it averages individual sightings, thereby reducing the denominator. According to Ginsberg and Young (1992), the twice-weight index tends to underestimate associations because it double counts the samples in which members of the pair are located separately. Cairns and Schwager (1987) suggested that the twice-weight index is the least biased when sampling favors the sighting of individuals A and B together. Finally, the simple index of association was considered by Ginsberg and Young (1992) to be the least biased of all the indices. They suggested that because it does not double the number of sightings in which both individuals are seen separately (i.e., twice-weight index), and does not decrease the denominator by averaging the number of sightings of each individual (i.e., half-weight index), that it is inherently the most accurate of the indices.

Most social foraging models focus on the direct fitness benefits of foraging in a group, such as increased detection of predators due to group vigilance (see reviews by Elgar, 1989; Lima & Dill, 1990; Quenette, 1990; Roberts, 1996), decreased risk of predatory attack due to dilution or confusion effects (see review by Roberts, 1996), and increased opportunities to find food resources (Caraco, 1981; Clark & Mangel, 1984; Giraldeau & Beauchamp,

1999; Ranta, Rita, & Lindstrom, 1993). Demonstration that indirect fitness effects may play a role in social foraging strategies would suggest that current models should be modified to include such effects, as they may change outcomes at both the individual and population levels.

Methods

Species and Study Area

Northwestern crows (*Corvus caurinus*) were observed foraging along the beach at Meadowdale Park, which fronts on Puget Sound, in Snohomish County, Washington (N 47°, W 122°) during all seasons of the year. Fifty-five crows were captured (Washington Department of Fish & Wildlife, Permit No. WM-0158; United States Department of the Interior, Fish & Wildlife Service, Permit No. 22802) at this park, in nonterritorial areas and using baits containing alpha-chlorolose tranquilizer (Stouffer & Caccamise, 1991) and a net gun (Day, Schemnitz, & Taber, 1980). We briefly restrained the animals (approximately 10 min) for banding and blood draw. DNA was extracted from approximately 150 μ l of blood taken from the wing vein of each bird. Each individual was marked with the US Fish & Wildlife aluminum band on one leg and one to three colored bands distributed in a unique combination over both legs. Captured birds were held in an animal carrier and kept warm until they were processed and had recovered from the sedation (if applicable), at which time they were released at the location at which they had been captured.

Sexing

Crows are not sexually dimorphic; thus, we determined sex using a polymerase chain reaction (PCR)-based assay of the absence (male: ZZ) or presence (female: ZW) of the W chromosome (Griffiths, Daan, & Dijkstra, 1996). The technique was validated using DNA samples from crows of known sex (two males, three females; 100% correct classification; binomial $p = 0.0312$).

Kinship Analyses

Microsatellites are simple sequence repeats of 1–6 bp that are common in eukaryotic genomes (Tautz, 1989). Their ease of assay via PCR, and the high levels of polymorphism (manifested by variation in

repeat number) of these codominant Mendelian markers, makes them powerful tools for determining relatedness (Queller & Goodnight, 1989; Queller, Strassmann, & Hughes, 1993). Primers for two tetranucleotide loci developed for the Mexican jay (*Aphelocoma ultramarina*; Li, Huang, & Brown, 1997) and for four dinucleotide loci developed for the Mariana crow (*Corvus kubaryi*; Tarr & Fleischer, 1998) were used to amplify six microsatellite loci in the study population and in an outgroup population. Generic amplification reactions consisted of 100 ng of template DNA, 0.3 μ M each of primers, 0.2 mM each dNTP, 1.5 mM $MgCl_2$, 0.05 U/ μ l of *Taq* DNA polymerase, and the 1X *Taq* buffer in a final volume of 10 μ l. Tetranucleotide loci were run on nondenaturing 6% or 8% polyacrylamide electrophoresis gels at 16 V/cm for 2–2.5 h.

The dinucleotide loci were analyzed on an Applied Biosystems Inc. (ABI) Perkin-Elmer 373-XL genotyper system. For each of these loci, one primer was fluorescently labeled and the amplified sequences were pooled into sets along with ABI Genescan 350 TAMRA internal lane size standards, denatured at 94°C for 5 min and loaded on a polyacrylamide gel. The data were analyzed using ABI Genescan software.

Pairwise relatedness calculations were produced with KINSHIP 1.2 (Goodnight & Queller, 1999) using all 55 birds that were captured. With this method, relatedness coefficients (r) range from -1.0 to $+1.0$. A negative coefficient indicates that the individuals share fewer alleles than expected given the background level of sharing in the population. Note that r is a measure of relative relatedness within the population. Thus, $r = 0.125$ does not necessarily imply a first-cousin relationship.

Social Affiliation Analyses

Analysis of association patterns and social structure were conducted by using the MATLAB program SOCPRO, written by Dr. Hal Whitehead of Dalhousie University (Whitehead, 1999). Coefficient of association (COA) indices were calculated for 28 crows sighted two or more times. There were several reasons for limiting the data sets to crows spotted two or more times, including preventing crows sighted only once from inflating mean levels of association by having a high number of COAs = 1.00, and ensuring that crows were distinctive enough to

be identified more than once over the course of the study.

The simple index (Cairns & Schwager, 1987) was used to determine associations between individuals and was calculated using the following equation:

$$\frac{x}{x + Y_{ab} + Y_a + Y_b}$$

where x is the number of times individual A and B are sighted in the same group; Y_a is the number of times only A is sighted; Y_b is the number of times only B is sighted; and Y_{ab} is the number of times A and B are seen separately. Permutation tests were performed to determine if the patterns of association between individuals differed significantly from random. These tests randomly generated alternative data sets containing the same number of crows and groups as the observed data (Bejder, Fletcher, & Brager, 1998). For the null hypothesis to be rejected, the distribution of observed association indices should be different from the distribution of random association indices (Bejder et al., 1998). To test for long-term companionship, we calculated individual associations within a sampling period of 1 day. If some individuals associated in different sampling periods more often than expected by chance, the standard deviations of the association indices would increase. Therefore, if the standard deviations of the observed association data were significantly higher than the randomly permuted data, then the null hypothesis of no preferred companions between sampling periods was rejected (Gowans, 1999).

Behavioral Sampling

Procedures (Individual or Focal Observations). The study was conducted from February 14, 1996 to August 19, 1998. All observation periods occurred between the hours of 0600 and 1400 h for a total of 223 h. All observations were conducted by R.R.H. The date and temperature were recorded at the start of each session. Individually marked crows were observed with 10 \times 25 binoculars. We randomly selected focal subjects from within groups of unmarked crows foraging within a meter of the waterline (Colwell & Landrum, 1993) and followed them for 5 min. Repeated sampling of the same individual was ac-

tively avoided by selecting subsequent subjects foraging away from the previous subject. During each 5-min period, the age class of the subject [adult vs. juvenile (first year)], subject and sex identification, outcome of each foraging trial (produce or scrounge by focal animal, loss of prey to another animal or unsuccessful acquisition of food), and the number of scrounge attempts made by the focal animal or number of scrounge attempts made on the focal animal by other animals were recorded on a laptop computer (Compaq Contura 486) using modified EVENT version 3.0 software (J. C. Ha), resulting in 2950 foraging trials. If a scrounge occurred in the trial, the level of aggressiveness (passive or aggressive) in an interaction, the direction of the theft, and the identity of interactors were recorded. Age class was determined by plumage color, tail rectrices, and mouth color of the bird (Pyle, Howell, Yunick, & DeSante, 1987). The breeding season was defined as March to August and the nonbreeding season was September to February.

Capture of a prey item could occur through producing or scrounging. Producing was defined as an animal searching the substrate for prey items (head down), probing and capturing a prey item. Scrounging was defined as taking a prey item from a producer. Passive scrounges were those in which no physical contact (such as pecking) or chasing occurred between the interactors and the individual who lost the prey item to a scrounger made no attempt to retrieve the item. Unsuccessful passive scrounges were situations in which an individual with a food item was approached by another individual with no physical contact or chasing and the approaching bird was unsuccessful at obtaining the prey item. Begging was associated with wing flicks, bowing, and specific vocalizations. Begging was not categorized as a scrounge in this study. Aggressive scrounges were those in which there was physical contact and/or chasing between the interactors either by the scrounger in an attempt to obtain the prey item or by the producer who lost the prey item to the scrounger. When an animal flew to a new location, but stayed in sight of the observer, focal animal sampling continued. Presence or absence of other foragers was recorded.

Focal sampling alternated with 30-s scan samples of the study site. During scan samples, we recorded the number of birds on the beach.

Procedures (Population Observations). This phase of the study was conducted from October 11, 1996 through November 1, 1998. All observation periods fell between the hours of 0600 and 1400 h for a total of 100 h. The date and temperature were recorded at the start of each session. Marked crows were observed with 10 × 25 binoculars. The observer performed a 30-s scan sample noting the number of crows on the beach and the identity of any marked individuals. Following the census scan, we conducted a 20-min period of all-occurrences sampling in which we noted every scroungeable item obtained by a crow, each scrounge attempt by another crow, whether or not the scrounge attempt was successful, whether the interaction was passive or aggressive, the interactor's identifications (if banded), and the direction of the scrounge (actor and recipient). A scroungeable item was defined as a food item that was large enough to be seen or that had a handling time that was long enough for observer detection (see Brockmann & Barnard, 1979 on the importance of food visibility in kleptoparasitism). A 30-s census scan was repeated at the end of the 20-min period.

Data Analysis

The variances were homogeneous, the distributions were normal, and recorded relatedness values were considered independent events. Levels of relatedness among marked birds within larger groups of unmarked birds were compared with *t*-tests. Each *t*-test analysis used a different null hypothesis and underlying statistical population, and thus no Bonferroni adjustments were required. Frequency data were analyzed with chi-square tests. Because several chi-square analyses were performed on the same underlying statistical population, an overall (fully saturated) log-linear analysis was used to protect statistical decisions from type I error inflation (Sokal & Rohlf, 1981). The relatedness and social affiliation values by age and sex class categories were analyzed with ANOVA. All comparisons were two-tailed.

Results

Social Affiliation Patterns

The observed association of individuals in the population was significantly different than random

($p = 0.0007$; see Table 1). Our data demonstrate significantly greater levels of association among females than among males, $t(20) = 3.08$, $p = 0.006$. However, females were not associating at levels greater than random expectation ($p = 0.120$), while males were associating nonrandomly ($p = 0.011$).

There was no difference in degree of association between adult and juvenile crows, $t(19) = 1.80$, $p = 0.087$. However, adults were associating nonrandomly ($p < 0.001$) and juveniles were associating randomly ($p = 0.813$).

Relatedness Patterns

The coefficient of relatedness will be abbreviated as r (Table 1). The overall average background relatedness of the population was near zero (mean $r = -0.0192$, SE ± 0.0004 , $N = 55$). Females sighted two or more times were related to one another by a mean relatedness of $r = 0.08146$ (SE ± 0.0353 , $N = 13$), while males sighted two or more times were related to one another by a mean relatedness of $r = 0.0277$ (SE ± 0.0301 , $N = 15$), $t(26) = 0.59$, $p = 0.56$. Adults sighted two or more times were related to one another by a mean relatedness of $r = 0.0378$ (SE ± 0.0211 , $N = 20$), while juveniles were related to one another by a mean relatedness of $r = -0.0438$ (SE ± 0.0499 , $N = 7$), $t(25) = 0.85$, $p = 0.40$.

Kinship, Sex, Age, and Scrounging

Numerous scrounge attempts were observed in which one or both of the interactors were unmarked

(Robinette & Ha, unpublished); only interactions with two marked birds were used in these analyses. This was a requirement so that we could calculate the relatedness and social affiliation between the interactors. The average relatedness between marked individuals involved in a food-stealing interaction (mean $r = -0.013$, range -0.450 to 0.449 , SE ± 0.042 , $N = 37$) was not significantly different from the background relatedness, $t(36) = 0.15$, $p = 0.88$. Overall, crows do not steal from, or avoid stealing from, relatives.

The mean relatedness of a scrounger to the other individuals in its foraging group (mean $r = 0.025$, SE ± 0.017 , group size 4–12 banded birds, mean = 6.62 banded birds) was not significantly different than the average population relatedness ($r = \pm 0.013$), suggesting that these larger foraging groups are not composed primarily of relatives, $t(36) = 1.47$, $p = 0.15$. Individuals did not select their scrounging targets randomly from the background relatedness of the foraging group (paired t -test for significant deviation between r of scrounging pair and the average background relatedness of the associated foraging group). Individuals that scrounged passively did not select scrounging targets that were more closely related to them (mean \pm SE = 0.056 ± 0.063 , $N = 20$) than the group average (0.031 ± 0.021 , $N = 20$), $t(19) = \pm 0.409$, $p = 0.687$ (Table 2). Individuals that scrounged aggressively did select scrounging targets that were less related to them (-0.094 ± 0.049 , $N = 17$) than their average relatedness to the foraging group

Table 1. Mean Social Association (Simple Index) and Mean Relatedness (r) by Sex and Age Class of Individuals Sighted Two or More Times

	All	Males	Females	Adults	Juveniles
Association					
Mean	0.11	0.08	0.14	0.13	0.07
SE	0.01	0.01	0.02	0.02	0.02
Min	0.03	0.02	0.03	0.01	0
Max	0.19	0.15	0.21	0.21	0.13
Significance (two-tailed t -test)			<0.01		0.09
Relatedness					
Mean	-0.01	0.03	0.08	0.04	-0.04
SE	<0.01	0.03	0.03	0.02	0.05
Min	-0.42	-0.40	-0.26	-0.40	-0.42
Max	0.73	0.68	0.73	0.60	0.39
Significance (two-tailed t -test)			0.56		0.40

Table 2. Relatedness in Foraging Groups

Interaction	Relatedness of Scrounger to Foraging Group (r)		Relatedness of Scrounger to Producer (r)	
	Mean	Range	Mean	Range
Passive	0.031	-0.162+0.155	0.056	-0.450+0.449
Aggressive	0.019	-0.224+0.269	-0.094	-0.450+0.204

Passive scrounges ($N = 20$) generally occurred between more closely related individuals, while aggressive scrounges ($N = 17$) occurred among less closely related individuals. However, the mean relatedness of the scrounger to its foraging group did not differ between passive and aggressive scrounges.

(0.019 ± 0.029 , $N = 17$), $t(16) = 3.677$, $p = 0.002$. The mean relatedness of individuals involved in aggressive encounters (-0.094) was not significantly less than the mean relatedness of individuals participating in passive interactions (0.056), $t(35) = 1.824$, $p = 0.077$.

However, when the sex of the interactors is added to the level of aggression in an analysis of the relatedness among interactors during a scrounge or scrounge attempt, same-sex food-stealing pairs were more related (0.0134 ± 0.063 , $N = 13$) than pairs of opposite sex (-0.100 ± 0.048 , $N = 22$), $F(1, 31) = 8.790$, $p = 0.006$, and the relatedness of the interactors was higher in a passive interaction (0.100 ± 0.053 , $N = 19$) than in an aggressive interaction (-0.066 ± 0.058 , $N = 16$), $F(1, 31) = 4.420$, $p = 0.044$. There was no significant interaction between interactor sex and level of scrounge aggression, $F(1, 31) = 1.610$, $p = 0.214$; $R^2 = 0.317$.

A similar analysis of the sex of the interactors and their age class (juvenile vs. adult) revealed that same-age interactors were significantly less related (-0.257 ± 0.066 , $N = 16$) than different-age interactors (0.049 ± 0.040 , $N = 19$), $F(1, 31) = 15.578$, $p < 0.001$, and there was a significant interaction between the sex and the age of interactors, $F(1, 31) = 26.415$, $p < 0.001$; $R^2 = 0.59$ (Fig. 1).

There was no significant effect of season (breeding vs. nonbreeding, $N_{\text{breeding}} = 16$, $N_{\text{nonbreeding}} = 21$) on the probability of a scrounge, $t(35) = 0.781$, $p = 0.44$, suggesting that the effect is not driven by parents feeding fledglings during the breeding season. Juveniles were no more likely than adults to participate in scrounges or scrounge attempts ($N_{\text{adult}} = 12$, $N_{\text{juvenile}} = 25$), $\chi^2(1) = 2.25$, $p = 0.1336$, and were no more likely to be successful compared with adults,

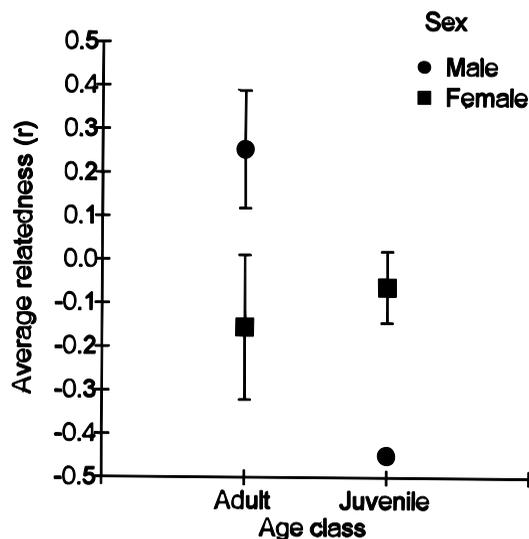


Figure 1. The average relatedness of interactors during a scrounge or scrounge attempt based on sex and age class. Error bars are ± 2 SE.

$\chi^2(1) = 0.69$, $p = 0.4056$. There was no significant difference between the level of aggression and whether the attempt was successful ($N = 12$) or not ($N = 25$), $\chi^2(1) = 2.33$, $p = 0.1270$. There was also no significant difference between the probability of a passive or aggressive scrounge or scrounge attempt and the age of the scrounger, $\chi^2(1) = 0.00$, $p = 0.9454$. There was no interaction between age, level of aggression, and the probability of a successful scrounge given an attempt, $\chi^2(1) = 0.35$, $p = 0.5517$. Finally, there was no relationship between the probability of a scrounge or scrounge attempt and the sex of the scrounger ($N_{\text{males}} = 19$, $N_{\text{females}} = 18$), $\chi^2(1) = 0.027$, $p = 0.869$.

Association Patterns and Scrounging

The level of association in foraging groups where a scrounge or scrounge attempt occurred was significantly higher (0.23 ± 0.012 , $N = 37$) than the background level of social association (0.11 ± 0.05 , $N = 23$), $t(35) = 19.17$, $p < 0.001$. However, there was no significant difference between the level of association in the foraging group where a scrounge or scrounge attempt occurred (0.23 ± 0.012 , $N = 37$) and the association between the producer and scrounger (0.239 ± 0.023 , $N = 37$), $t(35) = 0.048$,

$p = 0.962$, suggesting that the choice was not made on the basis of association within the group. There was also no significant difference between the association level when the scrounge interaction was passive (0.224 ± 0.03 , $N = 20$) or aggressive (0.258 ± 0.038 , $N = 17$), $t(35) = -0.709$, $p = 0.483$.

Discussion

The average relatedness between producer and scrounger interactors was similar to that of the overall population, and groups of foraging birds were not more closely related than the background relatedness of the population. However, when considering mean foraging group relatedness, passive scrounges tend to occur between more closely related individuals, and aggressive scrounges among less closely related individuals. Thus, scroungers may modulate their mode of scrounging according to relatedness, or producers may modulate their response, or both. When the sex of the interactors and the level of aggression were included in the analysis of the relatedness of the interactors during a scrounging attempt, same-sex pairs were more closely related than opposite-sex pairs, and the relatedness of interactors was higher in passive compared to aggressive interactions. Similarly, same-age interactors were significantly less closely related than different-age interactors, and there was an interaction between the sex and age of the interactors. Specifically, juvenile males were significantly less closely related compared to adult males, suggesting that scrounge interactions between adult males only occur when they are related to one another. This may reflect the likelihood that the risk of injury among adult males is much higher than among juvenile males. Lower relatedness in opposite-sex but same-aged interactors may reflect scrounging interactions of mated birds (Beauchamp, 2000). Certainly, the opportunity for scrounging is related to proximity to the producer, which is likely to be closer in mated pairs.

Crows in this population discriminated among individuals that vary in the proportion of alleles that they share with the actor. These findings cannot be explained by a dominance of males over females or adults over juveniles, because there was no significant effect on the probability of a scrounge based on these factors. Another possible explanation for passive scrounging might be simply that adults

(caregivers) are feeding fledglings. However, there was no relationship with season (breeding vs. nonbreeding) on the relationship between kinship and scrounging, even though different-age interactors were more closely related than same-age interactors. Thus, the two most likely explanations of scrounging—fledgling feeding or dominance—do not fully explain the patterns observed here. Additionally, passive and aggressive scrounges were equally successful. If fledgling feeding was driving the system, one would expect that passive scrounges would be more successful. If dominance were driving the system, one would expect that aggressive scrounges would be more successful. We found no evidence to support either of those explanations. Instead, ecological factors, most notably the opportunity to steal a valuable prey item, influences whether or not a scrounge is attempted (Robinette & Ha, 2001), but the relatedness between the individuals determines the aggressiveness of the interaction (passive vs. aggressive).

As is true of most corvids, this population demonstrates an affinity for specific social companions: the observed association of individuals in the population was significantly greater than random. Females demonstrated higher levels of association than males, but female association was, and male association was not, significantly different from a random sample of the overall population. This suggests that females spend more time in the company of other females than males spend in the company of other males, but that females are less likely to associate with specific other females. Likewise, juveniles were less likely to have specific preferred companions than were adults.

One obvious mechanism for kin discrimination in this population is familiarity, suggesting a rule of thumb that familiar individuals are more likely to be related to the scrounger. Thus, we explored the relationship between coefficients of relatedness and social affiliation. Foraging groups were more likely to be associated than the background population, but were not more likely to be related than the background population. There was no difference between the average association of the foraging group and the association between the scrounge interactors, or the average association between passive and aggressive scrounges. Therefore, it appears unlikely that individuals are using a simple “familiar” versus “unfamiliar” rule of thumb to make

decisions about from which individuals to attempt a scrounge and how to respond to potential scrounge attempts.

To our knowledge, this study is one of the first to incorporate measures of kinship into analyses of the factors influencing producing and scrounging behavior. We can describe our findings in an imaginary group of crows. Some members of the socially foraging group spend more time being vigilant (scrounging) than with their head down looking for food items (producing) (Robinette & Ha, 2001). One of these individuals sees a producing individual locate a prey item that can be pilfered (i.e., that is large enough to provide an opportunity) (Ha & Ha, in press). If the potential scrounger would not lose by scrounging (i.e., the producer is not related or otherwise important to the scrounger's life), then the scrounger might benefit from being aggressive in its attempt to steal the food. In that same situation, the producer would likely benefit by aggressively defending its find. On the other hand, if the potential scrounger is related (or mated) to the producer, aggression would appear maladaptive (given that they are foraging in groups because it is beneficial to do so). In this situation, these opportunists might be selected to approach the producer to see if they can usurp the food, perhaps by mutually evaluating their foraging success and energetic status.

To date, there have been few opportunities to integrate detailed observations of social foraging interactions with information on genetic relatedness (but see Hatch & Lefebvre, 1997; Sklepkovych, 1997). Here we demonstrate that indirect fitness effects influence the scrounging interaction. Crows discriminate between kin and nonkin in the method of scrounging and discriminate among individuals as preferred social companions. Whether or not these findings can be generalized to other social foragers is not clear at this time, although kin discrimination in birds is well known (Beecher, Medvin, Stoddard, & Loesche, 1986; Emlen & Wrege, 1986; Emlen, Wrege, & Demong, 1995; Hatch & Lefebvre, 1997; Medvin, Stoddard, & Beecher, 1993; Sklepkovych, 1997; Wright, 1998). This lays the potential foundation for indirect fitness benefits to influence social foraging strategies. If so, current models would require modification to account for the effect of kinship on predicting the use of alternative strategies at the level of the individual and the population.

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