



Effects of ecology and prey characteristics on the use of alternative social foraging tactics in crows, *Corvus caurinus*

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The producer–scrounger model assumes that producers are animals that search for food, and scroungers are animals that steal food found by producers. By following foraging decisions made by beach-foraging crows, we assessed individual variability in strategy use, variables influencing the finder's share (when defined as the probability of retaining a prey item in the presence of food theft behaviour) and the benefits and costs of producing and scrounging. Data were collected using focal and all-occurrences scan sampling. Results indicated that more individuals were likely to use both producing and scrounging tactics than to be 'pure' producers. No pure scroungers were documented. When producers obtained scroungeable items, scroungers attempted to steal the item 46% of the time. Forty-one per cent of attempted scrounges were successful. Thus, producers suffered a 19% loss rate of scroungeable items to scroungers, although producers had access to large numbers of small (nonscroungeable) items. Although there were significantly more scroungeable prey items available at lower tides, there was no significant relationship between prey density and scrounge attempts or actual thefts. No ecological factors (group size, temperature, time of day, season) or individual characteristics (age, sex) influenced the probability of retaining prey. Prey retention was determined only by characteristics of the prey items: larger prey items or those with longer handling times were most likely to be stolen.

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Foraging behaviour, particularly of highly cognitive animals such as corvids, primates and cetaceans, is frequently a social, even cooperative, activity. Thus, factors like kinship and strategic decision making, formerly considered of empirical interest only in studies of mating strategies and reproductive behaviour, are now proving of great value in investigations of the evolution and mechanisms of social foraging. Giraldeau & Caraco (2000) described the first coherent theory of social foraging, and our work follows their models, terminology and predictions closely.

We studied individually marked northwestern crows, *Corvus caurinus*, foraging and interacting in the marine intertidal zone, which provides a highly valuable food resource for these animals. We examined factors influencing the use of food-producing and food-stealing behaviours by using focal and all-occurrences sampling to record individual and social foraging behaviour, molecular genetic techniques to determine sex, and invertebrate sampling to document differences in prey characteristics (density, diversity, visibility and handling time) in our system, where recurring variation in tide height provides

an experimental system. Intertidal zonation provides comparisons of foraging behaviours at different prey densities and diversities, as documented by preliminary invertebrate sampling (Robinette & Ha 2000). The accessibility of the subject animals and the frequency of change in prey characteristics have allowed us to investigate many aspects of foraging in this highly social species (Robinette & Ha 1997).

Social Foraging and Food Stealing

Following suggestions from the literature (reviewed in Brockmann & Barnard 1979), we have reserved the term 'kleptoparasitism' for interspecific food stealing (which is relatively rare but does occur between crows and gulls on our study site), and instead focus on intraspecific food stealing among crows. This behaviour has received much theoretical interest, primarily in the form of the producer–scrounger game (Barnard & Sibly 1981).

The producer–scrounger model suggests that the proportion of animals producing (searching for food) and scrounging (consuming food found by producers) may be an evolutionarily stable strategy (ESS; Barnard & Sibly 1981). The producer–scrounger game was originally proposed to explain a wide variety of social interactions

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(Barnard 1984), and has been applied to foraging behaviour (Caraco & Giraldeau 1991, on minimizing the probability of energetic shortfall; Vickery et al. 1991, on maximizing intake rate). Although the models have been tested experimentally (Giraldeau et al. 1994; Koops & Giraldeau 1996; Beauchamp & Giraldeau 1997; Mottley & Giraldeau 2000), and numerous studies have been done on kleptoparasitism, both interspecific (Brockmann & Barnard 1979; Thompson 1986; Belisle 1998) and intraspecific (Steele & Hockey 1995; Bautista et al. 1998), no explicit field tests of the models have been completed to date. Steele & Hockey (1995) found that prey-stealing success increases with prey size and handling time in kelp gulls, *Larus dominicanus*. In addition, juveniles initiate steals more often.

Accumulating evidence leads to the assertion that ecological conditions influence the plasticity of foraging strategies (Brockmann & Barnard 1979; Caraco & Giraldeau 1991). The distribution of food (Rohwer & Ewald 1981; Theimer 1987; Benkman 1988), divisibility of food (Giraldeau et al. 1990), group size, group stability and presence or absence of predators may all influence the producer–scrounger equilibrium, and whether or not the equilibrium is adjusted between or within individuals. Giraldeau et al. (1990) suggested that the extent to which patches are divisible may determine the degree of specialization in the scrounger strategy, but Ranta et al. (1996) suggested that exclusive scroungers could never evolve, and that a conditional scrounging strategy was more likely. Specialization in food stealing has not been found in oystercatchers, *Haematopus ostralegus* L. (Ens & Cayford 1996), turnstones, *Arenaria interpres* (Whitfield 1985), or curlews, *Numenius arquata* (Ens et al. 1990). Nevertheless, Rohwer & Ewald (1981) demonstrated that exclusive scroungers may occur when scroungers can displace producers through strong dominance relationships.

Giraldeau & Caraco (2000) further developed these models of food stealing, demonstrating that, according to model predictions, the proportion of producers in the foraging group should be influenced by group size and the 'finder's share'. In seed-eating birds, the finder's share is that proportion of a food patch that can be consumed by the finder before scroungers arrive and start feeding at the food patch. This proportion is based on characteristics of prey distribution, spacing and geometry of foragers, and possibly other factors distinct from decisions made by the forager itself. Di Bitetti & Janson (2001) demonstrated that in wild capuchin monkeys, *Cebus apella*, the finder's share was a function of the amount of food in the patch and the time until others (scroungers) arrived, and that higher social status allowed monkeys to increase their total food consumed.

In our system, food occurs as discrete items with handling times ranging from near zero to tens of seconds. Thus, food items cannot be shared in the same sense. In this study, we examined the probability that a producer would retain a given prey item. Our aim was to describe the effect of ecology and prey characteristics on this probability. Specifically, we predicted that ecological variables that affect energy demand would alter scrounging

behaviour and the probability of prey retention by the producer. In our study, these ecological variables included air temperature, time of day and season (breeding versus nonbreeding). Furthermore, we measured the effect of group size, expecting to find a frequency dependence of scrounging behaviour and prey retention, with smaller groups providing too few opportunities for scrounging. We also measured the effect of the social status correlates of age and sex (Richner 1989), expecting that dominant individuals (males, adults) would be more likely to successfully retain their prey or steal the prey of others. Finally, we examined the effect of predator (bald eagle, *Haliaeetus leucocephalus*) presence, because the presence of a known crow predator (Robinette & Crockett 1999) might affect the levels of vigilance in the group (Robinette & Ha 2001) and thus affect the efficiency of scroungers.

METHODS

Species and Study Area

The distribution of northwestern crows extends from southern Alaska south along coastal Canada to southern Washington, U.S.A., although there is some debate about their range extending into coastal Oregon and the north tip of coastal California (Madge & Burn 1994), as well as their species status (Johnston 1961). As a species, they are highly social. They are typically described as smaller than the more common American crow, *C. brachyrhynchos*, produce a lower and hoarser call, and feed in the intertidal zone, river mouths and islands (Madge & Burn 1994). Their diet consists mostly of small intertidal invertebrates and larger invertebrates such as clams (Mollusca: Bivalvia), worms (Nemertea: Nereidae), shore crabs (Arthropoda: Decapoda) and snails (Mollusca: Gastropoda) (Robinette & Ha 2000), although they occasionally feed on Pacific sand lances (Robinette & Ha 1997) and salmon carcasses. Beyond the tidal zone, they are omnivorous, feeding on invertebrates, small vertebrates and human refuse. The sexes are monomorphic, and first year juveniles are duller and browner than the glossy-black adults (Butler et al. 1984).

We observed northwestern crows foraging along the beach at Meadowdale County Park, which fronts on Puget Sound in Snohomish County, Washington, U.S.A. This beach site contains approximately 700 m of shoreline, with an intertidal substrate of mud, sand and small rocks, a high beach of dry sand and a sand bar at very low tide. The beach area is backed by an evergreen-wooded parkland, surrounded by suburban residential property. Crows are commonly seen in all of the areas, and nest in the park woodlands.

Procedures

Banding

Fifty-three crows were captured and released (Washington Department of Fish & Wildlife Permit No. WM-0158; U.S. Department of the Interior, Fish &

Wildlife Service Permit No. 22802) at Meadowdale Park. Birds were captured using tranquilized baits (Stouffer & Caccamise 1991) and a net gun (Day et al. 1980). The animals experienced brief restraint (~10 min) for banding and blood draw. Each individual was marked with a U.S. Fish & Wildlife aluminium band on one leg and one to three coloured 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 recovered from the sedation, if applicable, then released where they had been captured.

Individual or focal observations

We conducted the study from 14 February 1996 to 19 August 1998. All observation periods fell between the hours of 0600 and 1400 (totalling 223 h). The date and temperature were recorded at the start of each session. Marked and unmarked crows were observed with 10 × 25 binoculars. Sampling consisted of focal and scan sampling. Focal animal sampling began with the selection of a subject from crows foraging within 1 m of the waterline (Colwell & Landrum 1993), and ended after 5 min of behaviour coding. Repeated sampling of the same individual was avoided by selecting subsequent subjects foraging away from the previous subject. During each 5-min period, we recorded the age class of the subject (adult versus juvenile, when available), subject and sex identification (when available), outcome of each foraging trial, time of day, search time (including time spent on foraging and vigilance), presence or absence of predator (Robinette & Crockett 1999), handling time and prey type on a laptop computer (Compaq Contura 486) using modified EVENT v. 3.0 software (J. C. Ha), resulting in 2950 foraging trials. Age class was determined by plumage colour, tail rectrices and mouth colour of the bird (Pyle et al. 1987). The breeding season was defined as March–August and the nonbreeding season was September–February.

Each focal observation period included one or more foraging trials, each of which was successful or unsuccessful. A successful trial consisted of the search time between the end of the consumption of one prey item (or the start of focal sampling) and the capture and consumption of another. An unsuccessful trial was the search time between the end of the consumption of one item and the departure of the animal from the study site. Capture of a prey item could occur through producing or scrounging. Producing was defined as an animal with its head down (searching the substrate for prey items, probing and capturing a prey item). Scrounging was defined as an animal with its head up (searching for opportunities to take a prey item from a producer). 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.

Search time for both producers and scroungers began when the subject made a forward motion subsequent to prey capture and consumption or when a focal observation period began and ended with the capture of another prey item (either by finding a food item in the substrate or by stealing a food item from another animal),

departure from the study site or end of the observation period. Handling time consisted of the time between the capture and complete consumption of the prey item. Prey type was recorded whenever possible. Both right- and left-censored trials (trials which, due to the sampling method, were either entered after the start of search behaviour or ended before capture of a prey item) were coded as censored to reflect loss of information and were dropped from all subsequent analyses.

Focal sampling alternated with 30-s scan samples of the study site. During scan samples, the number of producers and scroungers were recorded.

Population observations

This phase of the study was conducted from 11 October 1996 to 1 November 1998. All observation periods fell between the hours of 0600 and 1400 (totalling 100 h). The date and temperature were recorded at the start of each session. Marked and unmarked crows were observed with 10 × 25 binoculars. The observer performed a 30-s scan sample, noting the number of crows with the head oriented up and with the head oriented down. A 20-min period of all-occurrences sampling followed the census scan, during which we noted every scroungeable item obtained that was large enough to be seen or whose handling time was long enough for observer detection (Brockmann & Barnard 1979), each scrounge attempt and the time of day that it occurred, tide height, whether the scrounge was successful and the prey type. If either the producer or the potential scrounger was banded, the identity was recorded. Each scrounge attempt (whether successful or unsuccessful), once initiated, was followed to its conclusion. Thus, some scroungeable food items and resulting encounters may have been overlooked while the observer's focus was on the outcome of the preceding encounter. A 30-s scan of the number of birds in each head orientation was repeated at the end of all-occurrences sampling.

Sexing

Crows are not sexually dimorphic and thus were sexed on the basis of their DNA, which was extracted from approximately 150 µl of blood taken from the wing vein of each bird. Sex was determined using a PCR-based assay of the absence (male: ZZ) or presence (female: ZW) of the W chromosome (Griffiths et al. 1996). The technique was validated on DNA samples from crows of known sex ($N=2$ males, 3 females; 100% correct classification; binomial: $P=0.0312$).

Data Analysis

The height above mean low tide was calculated every 20 min using local tide tables and a custom computer program. Tide heights were blocked into three substrate zones, which were associated with differences in invertebrate prey distributions: 'low' sandy zone (<0.3 m); 'middle' wet sand and rock zone, containing green algae (0.3–2.0 m); 'high' dry sand tide zone (>2 m). Analyses were performed using general linear modelling,

Table 1. Prey density, scrounge attempt and success rates, and energy benefits associated with each prey item taken independently from the beach and stolen from other crows

	Prey encounter rate p_p	Scrounge attempt p_a	Attempt success p_s	Prey retention p_{pr}	Energy benefit				
					Biomass B_p (g)	Density e (kJ/g)	Search time (min)	Net energy E_n (kJ)	Net energy rate E_n/min
Bivalves									
Producer	0.0638	0.4640	0.3913	0.8184	0.2100	22.7700	1.7516	0.2498	0.1426
Scrounger							1.2671	0.0554	0.0437
Fish									
Producer	0.0221	0.7879	0.1923	0.8485	5.3333	22.5200	1.1993	2.2532	1.8788
Scrounger							1.9163	0.4023	0.2100
Crab									
Producer	0.0225	0.6139	0.4355	0.7326	0.0523	18.6300	1.2660	0.0161	0.0127
Scrounger							1.9473	0.0059	0.0030
Worms									
Producer	0.0100	0.3182	0.0000	1.0000	0.0250	16.8000	0.8988	0.0042	0.0047
Scrounger								0.0000	0.0000
Small*									
Producer	0.8815	0.0000		1.0000	0.0010	1.2000	0.6540	0.0011	0.0016
Scrounger								0.0000	0.0000

Biomass values for bivalves (Khalit 1996), fish (see Robinette & Ha 1997), crab (Szaniawska 1983), worms (see Robinette & Ha 1997) and small items (Percy 1979; Ryan 1986) were based on the values of average sizes from the literature and the size of those items at the study site. Energy density values adopted from Griffiths (1977).

*Averaged values of the energy provided by amphipods and barnacles.

incorporating discrete and continuous variables into the same model where possible. Multivariate analyses were performed whenever possible due to the power of analysing multiple independent variables simultaneously, as well as their interactions. We performed univariate tests when sample size was insufficient for multivariate analyses, primarily with measures like sex that required banded birds. The assumptions for these tests were met (Sokal & Rohlf 1981). The independent variables were tidal zone, group size, temperature, time of day, season (breeding or nonbreeding), age class (juvenile or adult), the presence or absence of predators (bald eagles), search time (whether producing or scrounging), handling time, prey item and the energy associated with prey items. The outcome of a trial (produce or scrounge) was the dependent variable in most analyses, but prey type and gross energy rate (energy (kJ) of prey item/(search+handling time)) were also treated as dependent variables. Outcome measures (produce or scrounge) required logistic regression with the outcome as the logistic (0/1) variable when independent variables were continuous. Dichotomous and categorical independent variables with outcome as the dependent variable were analysed with contingency table tests. Because fish were available only at extremely low tides, which occurred during the daylight hours only during the breeding season, we dropped them from analyses with tide height or season. Because fish were orders of magnitude more valuable in terms of energy (Robinette & Ha 1997), they were dropped from some analyses so that a comparison of the other items could be made.

Issues of collinearity were addressed by assessing the contribution that each variable made to R^2 , or the explained variance, and dropping a variable that contributed little (<1%) once the other variable was included. Autocorrelation within an individual focal animal sample (which might contain multiple foraging trials) was addressed by selecting only the first trial per sample for analysis. Trials that ended in a scrounge in the focal samples were rare, so all of these trials were included in the analysis. Given the low frequency of scrounging in focal samples, it is unlikely that pseudoreplication was a problem in this analysis, especially in the focal data, in which attempts were more easily made to avoid previously observed birds.

The average intake rates for producing and scrounging were calculated based on all prey items. This calculation included the probability of finding, stealing or losing prey and the gross energy rate associated with that particular prey type.

RESULTS

Frequency of Producing and Scrounging

During focal animal sampling, 2.5% of all successful foraging trials (including very small, nonscroungeable items) resulted in scrounging (Table 1). Individually marked birds ($N=26$) produced on 66–100% of their focal trials. The number of trials recorded for each bird ranged from 3 to 169 ($\bar{X} \pm \text{SE}=40.54 \pm 7.83$, $N=26$). During all-occurrences sampling, items had to be scroungeable to be

recorded, because these items were the only ones large enough to be consistently noticed by the observer during this type of sampling, and levels of producing by individually marked birds ($N=22$) ranged from 33 to 100% of these trials per individual, rather than the 66–100% suggested in observed focal samples. The number of trials recorded per individual during all-occurrences data collection ranged from 1 to 67 ($\bar{X} \pm SE = 15.86 \pm 3.38$, $N=22$). For subjects that were observed across both sampling techniques ($N=15$), eight subjects were never observed to scrounge and seven subjects used both producing and scrounging. No subjects demonstrated a pure scrounging tactic. There was no sex or age bias in the use of producer versus producer–scrounger tactics (chi-square test: sex: $\chi_1^2=0.077$, $P=0.782$; age: $\chi_1^2=0.045$, $P=0.833$).

Effects of Ecological Variables

Based on logistic regression of focal trials, there was no significant effect of group size (independent t test: $t_{546}=0.625$, $P=0.532$), temperature ($t_{545}=1.058$, $P=0.290$) or time of day ($t_{545}=0.492$, $P=0.622$) on the probability that a bird would retain its prey item. Contingency table analyses revealed that there was no significant effect of season on prey retention ($\chi_1^2=0.211$, $P=0.646$). Neither sex ($\chi_1^2=0.044$, $P=0.833$) nor age class of the subject (juvenile versus adult: $\chi_1^2=1.169$, $P=0.280$) predicted prey retention. There was no significant effect of the presence or absence of a predator on the probability of prey being stolen ($\chi_1^2=0.100$, $P=0.751$).

Effects of Prey Characteristics

Multivariate logistic analyses on the energy content, search time and handling time of all prey types (excluding fish), and the two-way interactions of these three main effects revealed a significant effect of energy content (independent t test: $t_{505}=7.859$, $P<0.001$), handling time ($t_{505}=4.054$, $P<0.001$), and the interaction between energy density and handling ($t_{505}=-4.118$, $P<0.001$) on prey retention. Trials that ended in a theft were associated with prey items of higher energy density and longer handling times. Specifically, bivalves (high energy) were stolen both before and after the shells were opened by the producer, and small invertebrates (low energy) were stolen when their handling times were long (i.e. barnacles). There was no significant effect of the search time on the probability that the trial would end in a theft, regardless of whether fish were included in the analysis ($t_{522}=-0.018$, $P=0.985$; not included: $t_{502}=0.193$, $P=0.847$).

The same multivariate logistic analysis of the effect of search and handling time on predicting prey retention for each prey type revealed no significant effect of search time for any single prey type. There was a significant effect of handling time on the probability of theft for small items ($t_{423}=2.973$, $P=0.003$).

During focal trials, fish ($\bar{X} \pm SE = 0.142 \pm 0.032$, $N=58$) and bivalves (0.142 ± 0.018 , $N=136$) were more likely to be stolen compared with worms (0.003 ± 0.059 , $N=17$),

crab (0.049 ± 0.031 , $N=56$) and small items (0.002 ± 0.008 , $N=1780$; $P<0.001$). Based on the all-occurrences sampling, where all scroungeable items were followed by the observer, some items were more likely to result in an attempted or successful scrounge than others (see Table 1). Scroungeable items were stolen in 19.0% of trials, resulting in a higher rate than revealed by the focal sampling (2.5%).

Interaction Between Prey Characteristics and Prey Density (Tide Height)

There was a significant difference in the availability of each prey type by tide height, blocked into metres ($\chi_1^2=178.73$, $P<0.001$), but logistic regression revealed no significant effect of tide height on prey retention, regardless of whether fish were included (independent t test: $t_{573}=-1.212$, $P=0.225$; not included: $t_{548}=-0.538$, $P=0.591$). There was also no effect of the tide direction (rising or falling) on the probability of a theft ($\chi_1^2=0.229$, $P=0.632$).

Effects of Gross Energy Content

Trials that ended in prey loss were associated with prey items, excluding fish, with higher gross energy content (4.541 kJ/min for scrounges and 0.348 kJ/min for trials ending in produce; independent t test: $t_{506}=-12.470$, $P<0.001$). The addition of fish to the analysis resulted in variances that were not homogenous and gross energy was log-transformed for this analysis. This analysis resulted in the same pattern of significantly higher gross energy for trials that ended in theft ($\bar{X}_{\text{scrounge}}=47.759$ kJ/min; $\bar{X}_{\text{produce}}=4.153$ kJ/min; independent t test: $t_{407}=-7.037$, $P<0.001$). Producers had higher gross energy returns on crab and worms compared with scroungers, but scroungers had higher gross energy returns on bivalves and fish (Fig. 1).

DISCUSSION

Focal animal sampling suggested that approximately 2.5% of foraging trials (including very small, non-scroungeable items) resulted in prey loss. This low percentage rate in our population may be misleading, because foragers are unlikely to be searching for small items due to their low rate of energy return. In fact, this rate may underestimate the importance of scrounging in this population because when crows find large items, they suffer theft attempts 46% of the time. Furthermore, items that are most valuable in terms of energetic density were lost to scrounging 19% of the time. Beach foraging may result in more variability in the quality and distribution of prey (i.e. from small amphipods to fish) compared with seed feeding. Crows often collect small energy-poor items, and these are rarely stolen, whereas energy-rich items are often stolen (Steele & Hockey 1995).

Neither ecological factors like ambient temperature, time of day, season and predator presence nor individual

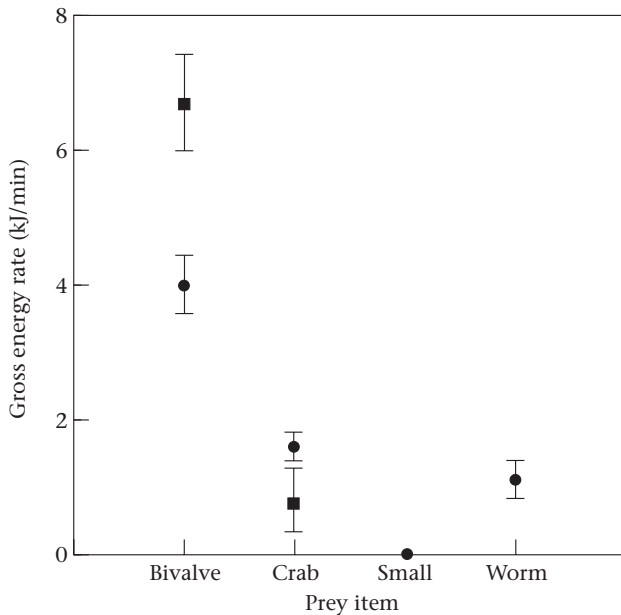


Figure 1. Average \pm SE gross energy rate of each prey type (excluding fish) based on the tactic used (circles: produce; squares: scrounge). The average \pm SE gross energy rate for fish: produce: 222.4 ± 39.3 kJ/min; scrounge: 237.2 ± 91.2 kJ/min.

characteristics like age or sex had an effect on the occurrence of scrounging. Scrounging was most productive, in terms of gross energy, and most likely to occur when the prey item was a bivalve or fish. Attempts on these two items were high (46% and 79%, respectively), although the success rates of those attempts varied (39% and 19%, respectively). Overall, 18% of bivalves and 15% of fish were successfully scrounged. Scrounge rates on bivalves were similar to those reported for mussel stealing in oystercatchers, in which the focal animal attacked and stole a mussel in 18.7% of trials (Goss-Custard et al. 1982). Although this similarity may be a coincidence, these numbers may reflect more fundamental characteristics of intertidal producing-scrounging systems, perhaps based on bivalve densities, their value to the animal and the degree to which they can be defended. Scrounging on small and cryptic invertebrates is not profitable or feasible, because they are consumed quickly.

Prey items vary significantly in distribution and quantity by tide height (Robinette & Ha 2000) and, in the present study, thefts varied by prey item, but not by tide height (prey density). Another measure of prey density is search time, the reciprocal of encounter rate, which also did not predict scrounging in this population. This may be due to differences in prey distribution: prey at high and moderate tides are small and cryptic but common. At low tides, prey are more widely scattered but of high content (Robinette & Ha 1997). Thus, at low tides, search times are long but the payoffs are large. We suggest that theft occurs when there is opportunity, and that intake rates can be maximized by combining producing behaviour with scanning for theft opportunities (Robinette & Ha 2001). We are currently using an agent-based modelling approach to generate predictions for future field testing.

We found no effect of dominance, measured by age class and sex, on the probability of prey retention in this population. In crows, males are generally dominant over females and adults tend to be dominant over juveniles (Richner 1989). Thus, we expected that males would be more likely to steal successfully from females, and adults from juveniles. Studies on Harris' sparrows, *Zonotrichia querula* (Rohwer & Ewald 1981) showed that subordinates are producers and dominants are scroungers; dominants fight with one another to defend good territories and subordinates fight with one another to join these territories. Although the dominant birds 'scrounge' from the subordinates, subordinates and dominants have approximately equal probabilities of surviving the winter. Hansen (1986) also found equal payoffs for hunting and stealing in bald eagles, and that small or young birds were more likely to hunt than steal. Di Bitetti & Janson (2001) found that capuchin monkeys with higher social status were more likely to range in front of the foraging group, to discover food item patches first and to receive a larger proportion of the food.

In other work with our study population, we found that scrounging behaviour is modified on the basis of kinship (Ha et al. 2003). Thus, dominance may be important in the scrounging interactions between nonrelatives, but the occurrence of scrounging between relatives in our population obscured the relationship between dominance and theft. More intensive observations during periods where scrounging is most likely to occur (perhaps when bivalves and fish are available) would help to determine further whether dominance affects the interactions of nonrelatives. For example, subordinates may adjust the time that they spend foraging for certain prey items, depending on their risk of being robbed by dominant animals, or maintain greater interindividual distances, reducing their chances of being scrounged upon, or be scrounged upon as often as dominants because they use different prey items.

A major difference between our system and others that have been used to test hypotheses about producing and scrounging is that, in our system, prey items are not divisible. Crows find single items and can either retain them for consumption or lose them to theft. This contrasts with the paradigm used by other researchers in which foragers locate a patch of small, easily consumed food items (like seeds), and other foragers can choose to share that patch with the finder, thus reducing the 'finder's share'. We propose that our measure of prey retention, the probability that a producer keeps its prey item and consumes it, is comparable to the more common use of the term 'finder's share'. We view the probability of prey retention as a probabilistic form of the finder's share. However, further empirical and mathematical research is required to determine whether this view is warranted, or whether foragers on single prey items follow a different strategy. We consider it important to develop empirical studies of social foraging in a broad range of species with attention paid to several issues: the degree of food patch divisibility (the single item prey issue), spatial relationships as they relate to social status and interaction and

relatedness and its effects on the costs and benefits of social foraging.

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