Social and ecological factors influencing vigilance by northwestern crows, *Corvus caurinus*

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Vigilance behaviour is thought to be largely controlled by the threat of predation on foragers. In addition, an inverse relationship between group size and vigilance has been documented repeatedly and is known as the group size effect. We suggest that groups of beach-foraging northwestern crows are vigilant for predators and for opportunities to steal ('scrounge') from conspecifics. We collected data using 5-min focal samples that recorded search time, scanning frequency and bout lengths, predator presence, prey type and theft. We also recorded group size, time of day, temperature, and tide height and direction, resulting in 2950 foraging trials. Results indicated that increased scanning during a trial predicted trials that would end in theft. Group size did not significantly influence the proportion of scanning in a trial, but scan bout length increased with increasing group size. This result is opposite to that predicted by the group size effect and suggests that more birds means more opportunities to scrounge or be scrounged upon. This rejection of the group size effect is most likely due to the trade-offs between group size and scrounging opportunities.

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Vigilance is thought to be largely controlled by the threat of predation on foragers, and has been shown to increase with increasing predation risk (Edmunds 1974). In addition, an inverse relationship between group size and vigilance has been documented repeatedly and is known as the group size effect (Lima 1995; Roberts 1996). There are two primary hypotheses explaining this inverse relationship (Roberts 1996). The many-eyes hypothesis (Pulliam 1973; Powell 1974) suggests that per-individual vigilance decreases with increasing group size (see reviews by Elgar 1989; Lima & Dill 1990; Quenette 1990). When there are more individuals foraging in a group, there are more eyes available for detecting predators, and any one individual may benefit by spending less time scanning and more time foraging. Alternatively, it has been proposed that group size reduces the risk of predation (by a dilution or confusion effect), thus increased group size might also result in reduced vigilance if there is less risk to the individual by being in a group (see review in Roberts 1996; Lima 1998).

Pulliam (1973) suggested that the benefit of being in a group is that it increases the probability that a predator will be detected prior to an attack. Of course, this information must be communicated to other members of the group in order for it to benefit individuals that did not detect the predator, and thus for grouping to be advantageous. This phenomenon is termed collective detection (Elgar 1989; Lima 1995; Lima & Zollner 1996). Lima & Zollner (1996) found that visual and spatial separation affected antipredatory vigilance in emberizid sparrows, specifically that the visual alarm signal was less effective with increasing spatial separation among group members. Lima (1994) suggested that multiple predator detections might be necessary to elicit flock departure in nondetecting birds when the species does not use alarm calls. However, other studies have found social transmission of predator detection (e.g. Godin et al. 1988). This effect may vary with the behaviour and ecology of the species and the modality of alarm signalling.

While numerous studies have documented a negative correlation between group size and scanning rates (see Caraco 1979; Hoogland 1979; Barnard 1980; Elgar & Catterall 1981; Sullivan 1984), few studies have tested the assumption that this result is due to a reduction in predator surveillance (Elgar 1989). In addition, some studies have found an increase in vigilance with increasing group size (Elgar & Catterall 1981; Elcavage & Caraco 1983; Elgar et al. 1984; Sullivan 1985). In his review, Elgar (1989) suggests that potential confounding variables include food density and quality, competition within the group, edge effects, individual variation in foraging ability, sex, age and dominance, distance from

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cover, time of day and ambient temperature. Additional variance may come from breeding status, presence of predators and observers, and habitat obstructions and visibility. Based on the assessment of these factors in previous studies, Elgar concludes that most studies fail to demonstrate adequately an unambiguous relationship between vigilance behaviour and group size. Here we address the influence of many of these social and ecological factors on the vigilance behaviour of beach-foraging crows (Robinette & Ha 2000).

It has been suggested that foraging and vigilance for predators are mutually exclusive behaviours and thus produce trade-offs (Lima 1986; Lima & Dill 1990). For example, a bird foraging for a worm has its head down, and thus, cannot scan its environment for predators and search for prey items simultaneously (but see Lima & Bednekoff 1999). Therefore, contexts where animals might spend more time foraging (during the breeding season, early in the day, at colder temperatures) might result in decreased levels of vigilance. Similarly, situations in which there are large groups of animals in the presence of decreased food availability generate a form of scramble competition for required energy, and a decrease in vigilance will result (Lima et al. 1999). Thus, food availability and group size will interact to influence levels of vigilance.

An exception to the trade-offs between foraging and predator vigilance may occur when scanning provides opportunities to kleptoparasitize, or steal, food from conspecifics (or heterospecifics, for that matter). We suggest that social foragers may scan to detect predators and/or for food-stealing opportunities (Barnard & Sibly 1981; Giraldeau et al. 1994; Beauchamp & Giraldeau 1996; Barta & Giraldeau 2000). In this case, we expect to find a positive relationship between vigilance and group size, reflecting the effect of greater numbers of food finders and thus food-stealing opportunities.

The producer–scrounger model predicts that the proportion of animals producing (searching for food) and scrounging (consuming food found by those producing) may be an evolutionarily stable strategy (ESS) (Barnard & Sibly 1981). Thus, the number of scrounging animals in a social foraging group should depend on the number of producing animals in that group (frequency dependence).

The producer–scrounger (PS) game was originally proposed to explain a wide variety of social interactions (Barnard 1984). Its specific application to foraging systems has occurred only recently (Caraco & Giraldeau 1991, on minimizing the probability of energetic shortfall; Vickery et al. 1991, on maximizing intake rate). Experimental tests of the models are even more recent (Giraldeau et al. 1994; Koops & Giraldeau 1996; Livoreil & Giraldeau 1997), although numerous studies have been done on kleptoparasitism or food piracy, both interspecific (Brockmann & Barnard 1979; Thompson 1986; Belisle 1998) and intraspecific (Steele & Hockey 1995; Bautista et al. 1998).

Beach-foraging northwestern crows feed on intertidal invertebrates such as clams, worms, shore crabs and snails (Robinette & Ha 2000). 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 long handling times and provide increased opportunities for other foragers to steal from the finder or producer (Barnard & Sibly 1981; Giraldeau et al. 1994).

In the present study, we examined the influence of potential confounding or contributing variables on the vigilance behaviour of beach-forging groups of northwestern crows. Specifically, we predicted that vigilance behaviour of crows would increase: (1) with decreasing tidal zone (increasing food availability: see Robinette & Ha 2000), (2) when not breeding, in adults, (3) later in the day, (4) with higher ambient temperatures and (5) in the presence of predators (bald eagles, *Haliacetus leucocephalus*: see Robinette & Crockett 1999). We also predicted that vigilance may be influenced by individual variability. In addition, we describe the relationship between group size, vigilance and scrounging opportunities and behaviour.

METHODS

Species and Study Area

We observed northwestern crows foraging along the beach at Meadowdale Park, which fronts on Puget Sound, in Snohomish County, Washington, U.S.A. (47°N, 122°W).

Procedures

Banding

We captured and released 53 crows (Washington Department of Fish & Wildlife Permit No. WM-0158; United States Department of the Interior, Fish & Wildlife Service Permit No. 22802) at Meadowdale Park in Snohomish County, Washington. Birds were captured using tranquilized baits (Stouffer & Caccamise 1991) or a net gun (Day et al. 1980). The animals experienced brief restraint (approximately 10 min) for banding and drawing blood. We marked each individual with the U.S. Fish & Wildlife Service aluminium band on one leg and one to three coloured bands distributed in a unique combination over both legs. We held captured birds in an animal carrier and kept them warm until they were processed and had fully recovered from the sedation (if applicable), at which time we released them at the location of capture.

Behavioural observations

We conducted the study from 14 February 1996 to 19 August 1998. All observation periods fell between the hours of 0600 and 1400 hours for a total of 223 h collected by one observer (R.L.R.). The date and temperature were recorded at the start of each session. Marked and unmarked crows were observed with 10 × 25 binoculars (40–50 m from subjects). The observer always wore a blue jacket, kept low to the ground and avoided unnecessary movement. Sampling consisted of focal and scan

sampling. Focal subjects were arbitrarily selected from crows foraging within a metre of the waterline (Colwell & Landrum 1993), and were followed for a 5-min period (foraging trial). Repeated sampling of the same individual was actively avoided by selecting subsequent subjects foraging away from the previous subject. During each 5-min period, the age class of the subject (adult versus juvenile), subject identification (when available), outcome of each foraging trial, time of day, vigilance behaviours (scanning frequency and duration), and the presence or absence of predators were recorded on a laptop computer (Compaq Contura 486) using modified EVENT version 3.0 software (James 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 presence of a predator was determined by the observer based on alarm calls and mobbing behaviour by crows (Robinette & Crockett 1999). The breeding season was defined as March–August and the nonbreeding season was September–February. A foraging trial began immediately after a bird's capture and consumption of a prey item, and the search time was the time between the start of a foraging trial and the capture of another prey item. 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, capturing and consuming a prey item. Scrounging was defined as taking a prey item from an animal with prey. 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. Both right- and left-censored trials (due to sampling method) were coded as such to reflect loss of information and were dropped from all subsequent analyses. Vigilance (or scanning) was defined as any time an animal had its head oriented up (beak level or pointed up) rather than down at the ground. Both frequency and duration of vigilance were recorded. Maintenance activities (e.g. preening and bathing) were not included in these analyses.

Focal sampling alternated with 30-s scan samples of the study site. These scan samples were used to determine the number of crows within the visual range of the focal bird and human observer. This encompassed all birds in an area in which any bird could observe the capture, or behaviours associated with the capture, of a scroungeable prey item and the predator detection behaviours or responses (alarm calls, mobbing and departure from the flock).

Sexing

Crows are not sexually dimorphic and thus were sexed on the basis of their DNA. DNA 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 (2 males, 3 females; 100% correct classification; binomial test: $P=0.0312$).

Data Analysis

The height above mean low tide was calculated every 20 min with the aid of local tide tables and a custom computer program. Tide heights were blocked into substrate zones, which were associated with differences in invertebrate prey distributions: the 'low' sandy zone (<0.3 m), the 'middle' wet sand and rock zone, containing green algae (0.3–2 m), and the 'high' dry sand tide zone (>2 m). We performed analyses using the general linear modelling (GLM) module in SYSTAT 7.0.1 for Windows. This technique allows the mixing of categorical and continuous independent variables in the same (multivariate) analysis. We performed multivariate analyses whenever possible due to the power of analysing multiple independent variables (noted by main effect F tests) simultaneously, as well as their interactions (noted by interaction F tests). We performed post hoc comparisons using Fisher's least significant difference (LSD) tests. We performed univariate tests (t tests) when sample size was insufficient for multivariate analyses. We performed a linear regression on the number of birds on the beach as a function of tide height (m). The assumptions for these tests, including homogeneous variances, 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; for marked birds), individual identification (for marked birds), sex (for marked birds), outcome of trial (produce or scrounge) and the presence or absence of predators (bald eagles). The dependent variables were the proportion of a trial scanning (total scanning time/total search time), and the mean length of a scan bout (total scanning time/frequency of scans). We addressed issues of collinearity 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. We addressed autocorrelation within an individual focal animal sample (which might contain multiple foraging trials) by selecting only the first uncensored trial per sample for analysis. Alpha was set at 0.05, and tests were two tailed.

RESULTS

Individuals (marked birds only) did not differ in the proportion of a trial spent scanning (ANOVA: $F_{25,143}=1.033$, $P=0.429$) or on the length of a scan bout (ANOVA: $F_{21,77}=1.450$, $P=0.122$). Thus, it is unlikely that the inclusion of more than one data point per bird biased the results (Leger & Didrichsons 1994). Dropping all but the first foraging trial in each focal sample resulted in 571 foraging trials of marked ($N=169$) and unmarked birds ($N=402$), collected on 102 days. There were 1–80 birds (mean=14.41; median=12.00) present at the site on any given day. Linear regression analyses revealed that there were significantly more birds present at lower tide heights ($R^2=0.11$, $F_{1,569}=70.424$, $P<0.001$).

The proportion of a trial spent scanning was significantly influenced by whether or not the trial ended in theft ($F_{1,523}=31.361$, $P<0.001$), the ambient temperature
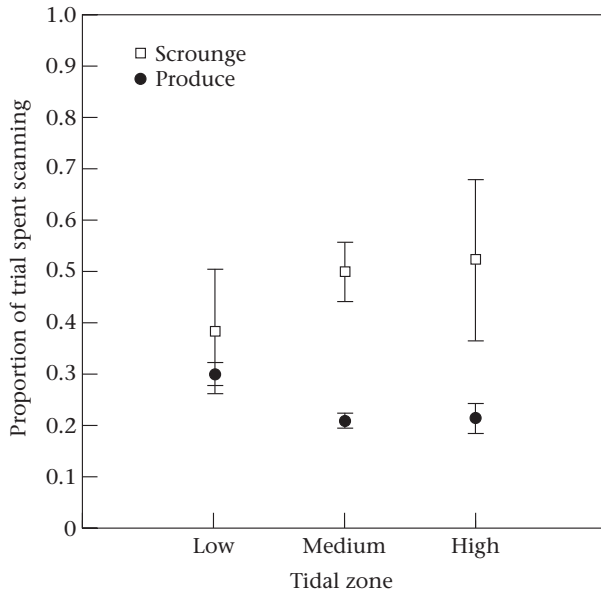
Figure 1. The mean (±SE) proportion of scanning as a function of tidal zone and the outcome of the trial (produce or scrounge). The proportion of a trial spent scanning was significantly influenced by whether or not the trial ended in theft and an interaction between theft and tidal zone.
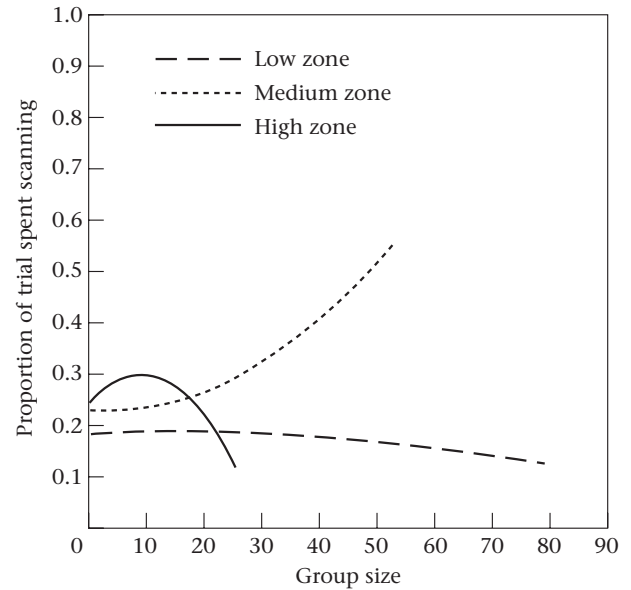

Figure 2. The proportion of a trial spent scanning as a function of group size and tidal zone. Although the overall influence of the number of birds on the beach (group size) was not significantly related to the proportion of a trial spent scanning, a multivariate analysis of scanning with both zone and group size as factors, revealed a significant effect of zone and near significant results for group size. The interaction between zone and group size was not significant.

($F_{1,523}$=5.427, P=0.020), and an interaction between theft and tidal zone ($F_{2,523}$=9.310, P<0.001). The proportion of a trial spent scanning was significantly higher when the focal animal scrounged ($\bar{X} \pm$ SE=0.439 ± 0.074) compared with when it produced (0.290 ± 0.014). Scanning increased with decreasing temperatures. When trials ended in a steal, the proportion of a trial spent scanning was higher in the middle ($\bar{X} \pm$ SE=0.497 ± 0.057; P<0.001) and high (0.521 ± 0.147; P=0.001) tide zones relative to the low zone (0.381 ± 0.116; Fig. 1). When trials ended in produce, the proportion of a trial spent scanning was highest in the low zone ($\bar{X} \pm$ SE= 0.299 ± 0.023) relative to the medium (0.207 ± 0.015; P<0.001) and high (0.213 ± 0.029; P<0.001; Fig. 1) zones. There was no significant effect of the number of birds on the beach ($F_{1,487}$=0.372, P=0.542), season ($F_{1,570}$=0.787, P=0.375), time of day ($F_{1,570}$=1.121, P=0.290), age class ($F_{1,172}$=2.607, P=0.108), sex (t_{154}=0.241, P=0.810) or the presence or absence of a predator (t_{570}= − 1.133, P=0.258) on the proportion of a trial spent scanning.

Although the number of birds on the beach (group size) was not significantly related to the proportion of a trial spent scanning, a multivariate analysis of scanning, with zone and group size as factors, revealed a significant effect of zone ($F_{2,567}$=4.807, P=0.009) and a near significant result for group size ($F_{1,567}$=3.481, P=0.063; Fig. 2). The interaction between zone and group size was not significant ($F_{2,565}$=1.619, P=0.199), but there is an inherent bias in this relationship because there were no large group sizes at high tide when prey were scarce.

The length of a scan bout (total scanning time/ frequency of scans) was significantly influenced by the tidal zone ($F_{2,318}$=5.381, P=0.005), the group size

($F_{1,318}$=7.850, P=0.005), with a pattern similar to that of proportion of trial spent scanning (Fig. 2), and an interaction between tidal zone and season ($F_{2,318}$=3.187, P=0.043). Scan bout was significantly shorter at the middle tidal zone ($\bar{X} \pm$ SE=1.548 ± 0.082 s) compared with the low (2.155 ± 0.163 s; P=0.002) and high (1.921 ± 0.145 s; P=0.027) zones. Scanning bout length increased with increasing group size. During the nonbreeding season, scan bouts were significantly longer in the low ($\bar{X} \pm$ SE=2.435 ± 0.292 s; P=0.005) and high (1.825 ± 0.156 s; P=0.023) zones compared with the middle (1.364 ± 0.135 s). There was no significant effect of time of day ($F_{1,329}$=1.793, P=0.181), temperature ($F_{1,327}$=0.000, P=0.990), age class ($F_{1,100}$=0.481, P=0.490), sex (t_{91}= 1.858, P=0.066) or the presence or absence of a predator (t_{329}= − 0.046, P=0.964) on the length of a scan bout. Scan bouts associated with trials that ended in theft were longer ($\bar{X} \pm$ SE=2.263 ± 0.272 s) than trials that ended in produce (1.789 ± 0.060 s) but the difference was not statistically significant (t_{279}= − 1.701, P=0.090). The interaction between zone and group size was not significant ($F_{2,325}$=1.629, P=0.198).

DISCUSSION

We failed to observe a decrease in vigilance with increasing group size, hence the group size effect was not supported in this population. We found that other factors, such as tidal zone and the opportunity to kleptoparasitize food from conspecifics had the greatest

influence on vigilance. The low tidal zone contains valuable, patchily distributed prey (e.g. sand lances) that require long handling times (see Robinette & Ha 1997, 2000). The middle tidal zone is rocky and prey are evenly distributed, while the high tidal zone has low prey densities (Robinette & Ha 2000). Thus, in this population, the proportion of time spent scanning and the length of a scan bout in a foraging trial increased with increasing prey quality and decreasing prey quantity. In our study, prey quality and quantity were restricted by natural invertebrate zonation patterns. Clearly, studies in which prey characteristics are manipulated experimentally will be necessary to understand these relationships more fully.

The proportion of a trial spent scanning was higher in trials in which a focal animal scrounged, but not in trials where predators were present. This suggests that in this population, scanning may be influenced more by the opportunity to steal, and perhaps by the avoidance of lost prey for producers. Scan bout length showed a similar pattern. This result is contrary to the scramble competition hypothesis, which predicts that increased competition for food results in a decrease in vigilance as individuals forage to obtain limited prey (e.g. Lima et al. 1999). However, in the present study, scroungers spent a larger proportion of time scanning than producers. This result supports the hypothesis that scroungers may provide increased group vigilance (Ranta et al. 1998).

Group size did not affect the proportion of scanning in a trial, but did affect the length of scan bouts. Contrary to the predictions of the group size effect, scan bout length increased with increasing group size. Our data suggest that more birds may mean more opportunities to steal and to be stolen from. While we have shown that trials that ended in a scrounge were associated with more scanning than trials where a producer found its own prey, our data do not reveal how scroungers affect the scanning of producers. It is likely that producers spend some time scanning in defence of scroungers. It is particularly revealing that a study on American crows, *Corvus brachyrhynchos*, found that vigilance decreased with increasing group size, but the birds were observed foraging in fields and lawns for worms and insects, which are not easily scroungeable (Ward & Low 1997). There was no significant effect of time of day, individual variability, age class or sex on the proportion of scanning or the length of scan bouts in this study.

Social foragers may be scanning for scrounging opportunities, or against scroungers (see Pravosudov & Grubb 1999 for a discussion of dominance and vigilance), in addition to scanning for predators. While reduced vigilance for predators in larger groups is a logical hypothesis, the presence of larger groups also may mean more scrounging opportunities and scrounging risk for foragers. Across all tide zones, scanning was relatively constant at smaller group sizes, suggesting that when scanning does occur, it is primarily associated with predator avoidance. But, in large foraging groups, when antipredator vigilance should be minimal, ecological variability in prey density and therefore, scrounging opportunities, determines the proportion of scanning in a foraging trial and the duration of a scanning bout.

Thus, scanning or vigilance behaviours were influenced by more than group size and the risk of predation. In response to Elgar's (1989) review we have addressed food density and quality (measured as tidal zone), competition within the group, individual variation in foraging ability, sex, age and dominance, time of day, ambient temperature, breeding status and the presence of predators. We found significant effects of tidal zone (prey density and quality), ambient temperature, season (breeding versus nonbreeding) and the probability of stealing on vigilance behaviour. The only significant effect of group size was in the direction opposite that predicted by the group size effect.

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