Increasing vulnerability to predation increases preference for the scrounger foraging tactic

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When animals forage in groups, individuals can search for food themselves (producer tactic) or they can search for and join other individuals that have located food (scrounger tactic). The scrounger tactic may provide greater antipredator benefits than the producer tactic because “scroungers” hop with their heads up and tend to occupy central positions in a group, whereas “producers” hop with their heads down and tend to occupy edge positions. We tested whether increasing an individual’s vulnerability to predation (using wing-loading manipulations) causes an increased preference for the scrounger tactic in zebra finches (Taeniopygia guttata). Wing-loading manipulations were effective at increasing focal individuals’ perception of vulnerability to predation; treatment individuals increased their total time allocated to vigilance, whereas control individuals did not. Treatment individuals also increased their use of the scrounger tactic (proportion of hops with head up) and scrounged a greater proportion of patches, whereas control individuals exhibited no changes. Our results are consistent with the hypothesis that the scrounger tactic confers greater antipredator benefits than the producer tactic, although whether antipredator benefits are achieved through differences in head orientation, spatial position, or both, remains unclear. Our finding that individuals adjust their use of the scrounger tactic according to changes in their phenotype provides evidence for phenotype-limited allocation strategies in producer–scrounger games. Key words: phenotype limited, producer–scrounger, social foraging, Taeniopygia guttata, vulnerability to predation, zebra finch. [Behav Ecol 19:131–138 (2008)]

Animals foraging in groups can search for feeding opportunities themselves (producer tactic), or they can search for opportunities to exploit the food discoveries of conspecifics (scrounger tactic). Both tactics are maintained in the group via negative frequency dependence because producer does better relative to scrounger when producer is rare and vice versa (Vickery et al. 1991; Mottley and Giraldeau 2000). The stable equilibrium frequency (SEF) of tactic use within a group is defined as the point where no individual can increase its fitness via a unilateral shift in tactic use (Mottley and Giraldeau 2000). Several factors influence where the SEF of a group lies, including patch distribution (Vickery et al. 1991; Livoreil and Giraldeau 1997), the extent to which the resource can be monopolized by the producer (Mottley and Giraldeau 2000), and group size (Vickery et al. 1991; Coolen 2002).

Most producer–scrounger foraging models predict the SEF level of investment in each tactic for the group but make no predictions regarding how each individual within the group should contribute to this SEF (Barnard and Sibly 1981; Vickery et al. 1991; Barta and Giraldeau 2000; Giraldeau and Caraco 2000). At the SEF, marked, yet long-lived individual differences in the relative use of alternative tactics may exist, so long as the SEF is met overall (Beauchamp 2001; Bugnyar and Kotrschal 2002; Ha RR and Ha JC 2003; Barta et al. 2004). Furthermore, individual differences may be maintained across different contexts (Koops and Giraldeau 1996; Beauchamp 2001), indicating that tactic use decisions may also be phenotype limited. Therefore, more recent empirical models of producer–scrounger foraging have attempted to include phenotypic constraints on tactic use (Ranta et al. 1996, 1998). Social dominance rank and foraging efficiency in particular have been studied explicitly with respect to individual differences in tactic use (Giraldeau et al. 1990, 1998; Barta and Giraldeau 1998; Liker and Barta 2002; Thibaudeau 2004; Beauchamp 2006). However, many of the factors that have been hypothesized to influence group-level investment in alternative tactics could equally be expected to influence individual tactic use decisions.

Here, we test whether an individual’s vulnerability to predation influences its allocation to producer–scrounger foraging tactics. Predation danger has previously been considered as a potential factor influencing producer–scrounger tactic use at the level of the group. Individuals using the scrounger tactic tend to hop with the head oriented upward (Coolen et al. 2001), and several studies have demonstrated that individuals that use foraging behaviors with a head-up orientation have greater inherent vigilance compared with those that use more head-down foraging behaviors (Elgar et al. 1986; FitzGibbon 1989; Barbosa 1995; Lima and Bednekoff 1999). In fact, disproportionately greater investment in vigilance for predators by scroungers has been suggested as a possible mechanism promoting the tolerance of scroungers within groups by producers despite their negative effect on foraging intake rate (Ranta et al. 1998). Furthermore, scroungers are more likely to be found in central positions in the group (Barta et al. 1997; Flynn and Giraldeau 2001), which tend to be safer compared with edge positions (Elgar 1989; Keys and Dugatkin 1990). Therefore, theoretical models have predicted that increased predation danger should increase the SEF of the scrounger tactic in the group (Barta and Giraldeau 2000). However, studies testing this prediction have yielded contradictory results. In northwestern crows (Corvus caurinus; Ha RR and Ha JC 2003), the presence of predators had no effect on scrounger tactic use. Similarly, in flocks of nutmeg mannikins (Lonchura punctulata), experimentally increasing the perceived
risk of predation by increasing the distance between the foraging site and protective cover had no effect on the relative use of the scrounger tactic (Coolen and Giraldeau 2003). In contrast, studies in free-ranging ravens (Corvus corax; Bugnyar and Kotrschal 2002) and tree sparrows (Passer montanus; Barta et al. 2004) reported higher use of scrounger tactics in groups foraging under increased predation risk, although in both cases mechanisms other than antipredator benefits of scrounging may have accounted for the shift.

Therefore, it remains unclear to what extent the use of the scrounger tactic may confer the individual that uses it greater antipredator benefits compared with the use of producer. If either head orientation or spatial position in a group influences predation risk, then differences among individuals with respect to vulnerability to predation are likely to influence tactic use decisions. We used a paired repeated measures design to test whether the use of producer and scrounger tactics at the level of the individual is mediated by vulnerability to predation. We experimentally increased the vulnerability to predation of focal individuals using wing-loading manipulation, whereas control individuals received sham manipulations. Wing loading, defined as mass per unit area of wing, is related to escape performance; higher wing loading reduces escape performance (Pennycuick 1975, 1989; Bednekoff and Houston 1994; Bednekoff 1996). Therefore, we used wing area reduction to increase experimentally an individual’s vulnerability to predation. We predict that if scrounging provides greater antipredator benefits compared with producing, then an experimental increase in wing loading should lead to an increase in an individual’s relative use of the scrounger tactic.

METHODS

Study subjects and aviaries

Commercially purchased zebra finches were maintained on a 12:12 h light:dark cycle (lights on from 0600 to 1800 h) at temperatures between 22 and 24 °C in same-sex groups with ad libitum access to water at all times. Outside of experimental periods, the birds were housed together in cages (115 × 61 × 90 cm high) with ad libitum access to vitamin-supplemented commercial millet seed mixture.

During experiments, 8 flocks of 8 randomly selected birds from a colony of 54 female zebra finches were placed into an indoor aviary (1.5 × 3.8 × 2.3 m high). We used female-only groups because female birds undergo large fluctuations in wing loading during egg laying and incubation (Moreno 1989; Veasey et al. 2001; Kulberg et al. 2005), making manipulations of wing loading a biologically relevant treatment for females. Some individuals were used in more than one group; however, a single, randomly selected, focal individual was observed per flock and focal individuals were never used in more than one group. Each bird was identified with a unique combination of 2–1 color leg bands.

Each aviary contained 2 large perches and a foraging grid that consisted of 2 side by side plywood boards with a combined dimension of 2.0 by 1.2 m, in which a total of 198 wells 1.3 cm in diameter, 0.8 cm deep, and spaced at 10-cm intervals were drilled. Foraging grids were placed on tables approximately 90 cm above the aviary floor, which allowed a seated observer to videotape the birds through a 1-way mirror using an 8-mm color camcorder mounted on a tripod. The foraging grid was covered by a sheet of black plastic at all times except during the foraging trials. The perches were placed at the far end of the aviary so that birds could not see directly into the wells from the perches but had to fly down to the foraging grid to search for food.

Experimental procedure

Birds were given 2 days to become familiar with the aviaries. Food was removed at 1800 h on the evening of the second day and each evening thereafter (evenings 2 through 10). Trials commenced at 0830 h the following mornings (days 3 through 11). Thus, the birds were deprived of food during the 12-h dark phase, plus an additional 2.5 h after lights on, durations that were necessary given that they store seeds in their extensible crops for overnight use.

Foraging trials were conducted for 9 days (days 3 through 11) 5 times per day at 1-h intervals. During each foraging trial, 10 millet seeds were placed in each of 15 randomly selected wells. Trials typically lasted circa 5 min, after which time all the patches on the foraging grid had been exploited and the birds returned to the perches. Birds were given ad libitum access to food after the final foraging trial each day (from 1240 to 1800 h).

The first 3 days of foraging trials (days 3–5) were used to train the birds on the seed distribution and were not videotaped. The following 6 days of foraging trials were videotaped as the observer (K.J.M.) called out the location of individuals into the audio channel of the videotape recorder to facilitate the identification of the focal individual during the playbacks from which data were recorded. Days 6–8 provided premanipulation behavior levels, and days 9–11 provided postmanipulation levels. Manipulations were carried out after the last foraging trial of day 8, with groups being randomly assigned to either experimental (n = 4) or control (n = 4) treatments.

Body mass was measured once a day at 0730, 1240, or 1800 h by placing the bird in a paper bag and weighing it on a digital balance to 0.01 g. The weighing time of day for each bird was randomized on condition that every 3 days each focal bird was weighed once at each of the 3 time periods.

Manipulation of vulnerability to predation

Prior to the start of experiments, digital photographs were taken of each focal bird’s right wing, stretched in a standardized manner over a sheet of white paper on which a 1 cm² area was clearly identified. Individuals randomly assigned to be in the experimental treatment had the tips of their 5 outer primary feathers of both wings clipped circa 5 mm, and their right wing rephotographed in the same manner as described above. Individuals assigned to the control treatment were handled in the same way but received sham feather clippings.

Digital photographs were analyzed using GNU Image Manipulation Program 2 (http://www.gimp.org) to calculate the surface area of the right wing in square centimeter. Photographic files were coded so as not to reveal the identity or treatment of the subject, although individuals assigned to the experimental treatment were obvious postmanipulation because their wing tips were blunt after feather clipping. Total wing area was estimated as twice the surface area of the right wing. Wing loading was calculated as follows: estimated total wing area (right wing area × 2) divided by the average body mass value during foraging trials ((mass[0730] + mass[1240] + mass[1800])/2) for both pre- and postmanipulation wing areas and mass values.

Video analysis

Data were recorded from the first 1 min of observations of video playbacks of trials playing at 1/5 speed using Noldus Observer 5.0 Video Pro. Videos were observed in random sequence by an observer that was blind to the treatment condition. The following behaviors were recorded: hop with head
Table 1
Three-stage nested factorial analysis results for measures of vigilance

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>df</th>
<th>F ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Dependent variable: scans/min</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Treatment</td>
<td>13.1712</td>
<td>13.1712</td>
<td>1</td>
<td>0.0536</td>
<td>0.8246</td>
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<td>Observation period</td>
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<td>616.237</td>
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<td>27.8955</td>
<td>0.0019</td>
</tr>
<tr>
<td>ID (treatment)–random</td>
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<td>245.782</td>
<td>6</td>
<td>51.1259</td>
<td>0.0049</td>
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<tr>
<td>Observation period × treatment</td>
<td>26.2663</td>
<td>26.2663</td>
<td>1</td>
<td>1.1890</td>
<td>0.3174</td>
</tr>
<tr>
<td>Observation period × ID (treatment)–random</td>
<td>132.546</td>
<td>22.9099</td>
<td>6</td>
<td>3.8533</td>
<td>0.5347</td>
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<tr>
<td>Error</td>
<td>5924.0444</td>
<td>26.4477</td>
<td>224</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Dependent variable: mean scan duration (s)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
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<td>10.4414</td>
<td>0.0179</td>
</tr>
<tr>
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</tr>
<tr>
<td>Error</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>C. Dependent variable: arcsine square root proportion of time scanning</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
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<td>Observation period</td>
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<td>16.5428</td>
<td>0.0017</td>
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<td>1.51663</td>
<td>0.00677</td>
<td>224</td>
<td></td>
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</tr>
</tbody>
</table>

up, hop with head down, produce patch, scrounge patch, scanning, off grid, and others.

Hopping with head up was defined as all jumps made with the head oriented such that a line drawn from the eyes through the nares would be parallel to the horizon or higher. When the projected line was below the horizon, the focal individual was scored as hopping with the head down. An individual was scored as having produced a patch when it was the first to encounter and feed at a patch. Individuals that moved rapidly toward a patch with at least one other bird already there were scored as scrounging the patch, irrespective of whether it subsequently fed from the patch or not. Scanning was scored when a stationary bird held its head up. All time spent off the foraging grid (on the perches, on the table, or on the floor beneath the table) was recorded. All other behaviors were pooled together as “others.” For each trial, the following values were calculated: scanning rate (number of scans per minute on foraging grid), mean scan duration, proportion of time spent scanning, proportion of hops with the head up (hops with head up/[hops with head up + hops with head down]), and proportion of patches scrounged (number patches scrounged/[number patches produced + number patches scrounged]). Proportion data were arcsine square root transformed prior to statistical analyses.

Statistical analyses

Separate paired t-tests were carried out on the wing area and wing-loading values obtained before and after manipulations for both control and experimental birds. Although we had a priori expectations regarding the direction of change in wing area and wing-loading values for experimental birds (decreased wing area and increased wing loading), we present the more conservative 2-tailed statistics. Tests for control birds were also 2-tailed.

Body mass values were compared within individuals before and after manipulations using a 4-stage nested factorial analysis (Montgomery 2005). The random effect, “ID,” was nested within treatment, whereas all fixed effects (“treatment,” “observation period,” and “time of day”) occurred in a factorial design. Behavioral data (scans per minute, mean scan duration, proportion of time scanning, proportion of hops with head up, and proportion of patches joined) were analyzed using 3-stage nested factorial designs (Montgomery 2005). The random factor, ID, was nested within treatment type whereas treatment type and observation period were arranged in a factorial. Full models are provided in Tables 1 and 2.

We used a paired experimental design because the high variation in tactic use between individuals means that very large samples of individuals would be required to detect differences between groups of different individuals. Using a paired design, each individual served as its own control, increasing our power to detect an effect of treatment with modest sample sizes. Because background values of tactic use were always obtained from treatment individuals prior to manipulation, control individuals were necessary in order to demonstrate that changes in tactic use among treatment individuals were not the result of some temporal effect. Therefore, the critical test given our experimental design is whether the change in tactic use between pre- and post observation periods varies depending on the treatment type received (treatment × observation period). Because statistical tests have reduced power to detect significant interactions (Littell et al. 1991), Tukey’s HSD post hoc tests controlling for multiple comparisons were used to test for 1) the effect of manipulation on experimental birds and 2) the effect of sham manipulations on control birds wherever the treatment × observation period interaction had a $P < 0.10$. In all cases, models included significant nested effects. However, as we are not interested in differences due to individuals, results for these effects are not discussed further. Values presented throughout the text are means ± standard errors.

RESULTS

Wing area, body mass, and wing loading

The total wing area of birds prior to wing area manipulations varied from 30.37 to 37.13 cm². Wing area manipulations significantly reduced the wing area of experimental (2-tailed
paired t-test, t-ratio = 5.45, P = 0.012) but not control (2-tailed paired t-test, t-ratio = 1.34, P = 0.27) individuals. Wing area decreased by 13.45 ± 2.39% (range 10.72–20.58%) in experimental individuals compared with 1.20 ± 0.91% (range −0.61% to 3.18%) in control individuals.

There were no significant interactions between treatment, observation period, or time of day (all P > 0.30) for body mass. Body mass did not differ between treatment types (F₁,₆ = 1.65, P = 0.25). However, body mass did differ according to time of day (F₂,₁₂ = 96.88, P < 0.0001) and observation period (F₁,₆ = 15.39, P = 0.0078) (Figure 1). Within observation periods, body mass did not differ significantly between 0730 and 1240 h measurements (Tukey’s test: Q = 2.67, P > 0.05) but was significantly higher at 1800 h (Tukey’s test: Q = 2.67, P < 0.05), just after the period of ad libitum feeding. For a given time of day, body mass measures were higher in the postmanipulation phase of the experiments.

The combined effect of changes in body mass and wing area resulted in a 25% increase in wing loading for experimental birds (Figure 2). The effect was significant (2-tailed paired t-test, t-ratio = 5.52, P = 0.011). Although the increase in body mass between pre- and postmanipulation phases of the experiment meant that wing loading tended to increase also in control individual after manipulations (mean increase 5.5 ± 3.14%, range −0.11% to 11.62%), this effect was not significant (2-tailed paired t-test, t-ratio = 1.73, P = 0.18).

### Scanning and scrounging behavior

There was no interaction between observation period (pre- or postmanipulation) and treatment type for scanning rates (treatment × observation period; F₁,₆ = 1.19, P = 0.32) (Table 1, Figure 3a). Scanning rates increased from 18.89 ± 1.06 to 22.10 ± 1.06 scans/min after either control or experimental manipulation (F₁,₆ = 27.90, P < 0.01). Within each observation period, there were no differences in scanning rates between control and experimental individuals (F₁,₆ = 0.05, P = 0.82).

There was a significant interaction between observation period (pre- or postmanipulation) and treatment type for mean scan duration (treatment × observation period; F₁,₆ = 10.44, P = 0.02) (Table 1, Figure 3b). Post hoc analyses indicate that experimental individuals significantly increased their mean scan duration after manipulation (Tukey’s test: Q = 3.46, P < 0.05), from 0.45 ± 0.07 to 0.54 ± 0.07 s, a 25% increase in mean scan duration. There was no change in the mean scan duration of control individuals (Tukey’s test: Q = 3.46, P > 0.05).

The effect of observation period (pre- or postmanipulation) on the proportion of time spent scanning also differed as a function of treatment type (treatment × observation period: F₁,₆ = 6.54, P = 0.04) (Table 1, Figure 3c). Post hoc analyses...
indicate that experimental individuals significantly increased the proportion of time spent scanning after wing manipulation (Tukey's test: $Q = 3.46, P < 0.05$), from $0.13 \pm 0.03$ to $0.20 \pm 0.03$, a 50% increase in time allocated to scanning. In contrast, there was no change in the proportion of time spent scanning among control individuals (Tukey's test: $Q = 3.46, P > 0.05$).

Differences in the proportion of hops with head up between pre- and postmanipulation phases of the experiment differed according to treatment (treatment \times observation period: $F_{1,6} = 4.99, P = 0.067$) (Table 2, Figure 4). The wing-loading manipulation resulted in a significant increase in the proportion of hops with the head up in experimental individuals (Tukey's test: $Q = 3.46, P < 0.05$), from $0.32 \pm 0.12$ to $0.48 \pm 0.12$, a 50% increase in scrounger tactic use. In contrast, manipulations had no effect on scrounger tactic use in control individuals (Tukey's test: $Q = 3.46, P > 0.05$).

Similarly, differences in the proportion of patches scrounged between pre- and postmanipulation phases of the experiment differed according to treatment (treatment \times observation period: $F_{1,6} = 11.38, P = 0.015$) (Table 2, Figure 5). Coincident with the increased use of “hopping with head up,” there was also an increase in the proportion of patches scrounged in experimental individuals after manipulation (Tukey's test: $Q = 3.46, P < 0.05$), from $0.56 \pm 0.08$ to $0.73 \pm 0.08$. Again, manipulations had no effect on the proportion of patches scrounged in control individuals (Tukey's test: $Q = 3.46, P > 0.05$).

**DISCUSSION**

We tested whether changes in an individual’s perceived vulnerability to predation influence its allocation decision to alternative social foraging tactics. We found that increased wing loading significantly increased an individual’s perception of vulnerability, as evidenced by the increase in proportion of time spent scanning in experimental individuals after manipulations, compared with control individuals, who showed no change in time allocated to scanning. Experimentally manipulated individuals also increased their investment in the scrounger tactic and consequently scrounged a greater proportion of patches than controls. These results are consistent with the hypothesis that scrounger provides greater antipredator benefits than producer. Furthermore, the finding that changes in the condition of an individual influence its use of producer or scrounger shows that these decisions can be phenotype limited.

Increased wing loading has been reported to increase vulnerability to predation in various avian species (Marchetti et al. 1995; Burns and Ydenberg 2002; Kullberg et al. 2005). Recently, however, some authors have called into question whether or not natural variation in wing loading influences predator escape performance, given that most studies that have reported an effect have manipulated wing loading beyond the usual range found in natural populations (van der Veen and Lindström 2000). Although the magnitude of our wing-loading manipulation is large (ca. 20% increase), it remains well within the scale of changes in wing loading that would be experienced by female birds during egg laying.
Our findings that birds with experimentally increased wing loading showed increases in scanning rates, mean scan duration, and proportion of time spent scanning are all indicative of increased wing loading resulting in an increased perception of vulnerability to predation. Although control birds increased neither their mean scan duration nor their proportion of time spent scanning, we did record an increase in scanning rate among our control birds after manipulation. It is not clear why control birds increased their scanning rates during the postmanipulation phase of the experiment; however, regular disturbance in the aviaries while carrying out the experiments (entering to place seeds in the foraging grids, removing food at night, and capturing birds for daily mass measurements) may have resulted in a general increase in weariness throughout the experiments for both control and experimental birds irrespective of treatment type. However, the magnitude of the increase in scanning rate was small (<3 additional scans per minute) and did not result in any increase in the time invested in scanning behaviors. Therefore, given that only experimental birds showed an increase in mean scan duration and proportion of time spent scanning, we conclude that the change in perceived vulnerability to predation was significantly greater in experimental birds than control birds after wing-loading manipulations.

We predicted that vulnerability to predation might influence individual allocation strategies to producer and scrounger foraging tactics. When individuals use the producer tactic, they tend to hop with the head oriented downward and are more likely to be found on the periphery of their foraging group, compared with scroungers, which hop with their heads oriented upward (Coolen et al. 2001) and tend to occupy central positions in the group (Barta et al. 1997; Flynn and Giraldeau 2001). Both head orientation while foraging and position within a group can influence vulnerability to predation. More head-up foraging behaviors have been demonstrated to provide increased predator detection abilities compared with head-down foraging behaviors in several species (Elgar et al. 1986; FitzGibbon 1989; Barbosa 1995; Krause and Godin 1996; Lima and Bednekoff 1999). Also, birds occupying central positions in flocks are less likely to be captured by predators (Petit and Bildstein 1987; Keys and Dugatkin 1990).

Consistent with our predictions, experimental birds significantly increased their use of the scrounger tactic (hopping with the head up), resulting in a larger proportion of scrounged patches (50% and 30% increase, respectively), whereas no change was observed in control birds. Although we attribute this shift in tactic use to the increased perceived vulnerability to predation of experimental birds, an alternative explanation for the increased use of the scrounger tactic is that the wing-loading manipulations may have resulted in an increased energy expenditure among experimental birds due to higher energetic cost of flight with increased wing loading (Pennycuick 1975, 1989). However, if increased energy expenditure leads to a decreased probability of meeting daily energy requirements, then we would predict a shift toward increased use of the producer tactic among experimental birds (Koops and Giraldeau 1996). Therefore, we conclude that increased perceived vulnerability to predation remains the most likely explanation for the increased use of scrounger tactic in experimental birds.

Our results differ from those of both Coolen and Giraldeau (2005) and Ha RR and Ha JC (2003) who report no effect of predation danger on the SEF of scrounging in nutmeg mannikins and northwestern crows, respectively. However, in both these studies, the whole group was exposed to variations in predation danger. When all group members simultaneously experience an increase in predation danger, they cannot all increase their use of scrounger without suffering a concomitant decline in foraging returns resulting from overuse of the scrounger tactic within the group. It is possible that balancing foraging returns and predation danger concurrently mitigates the effects of increasing predation danger on the group’s mean use of the scrounger tactic. Our manipulations altered the condition of a single individual per flock of 8 birds and therefore would have influenced to a relatively smaller degree the foraging payoffs to the scrounger tactic and hence the

![Figure 4](https://example.com/figure4.png)

**Figure 4**
Proportion of hops with head up for control and experimental focal individuals both before (pre) and after (post) manipulations. Each symbol and associated error bars represent the mean and standard error for a different focal individual. Lines connect the pre- and postvalues for the same individual. Note that graph depicts raw data, whereas statistical analyses were carried out on arcsine square root transformed data.

![Figure 5](https://example.com/figure5.png)

**Figure 5**
Proportion of patches joined for control and experimental focal individuals both before (pre) and after (post) manipulations. Each symbol and associated error bars represent the mean and standard error for a different focal individual. Lines connect the pre- and postvalues for the same individual. Note that graph depicts raw data, whereas statistical analyses were carried out on arcsine square root transformed data.
group’s use of tactics. We argue that differences between our results and those of Coolsen and Giraldeau (2003) and Ha RR and Ha JC (2003) highlight the importance of differentiating between group-level effects and effects at the level of the individual in frequency-dependent games.

Increased incidences of scrounging under higher predation danger have nonetheless been reported in both sparrows (Barta et al. 2004) and ravens (Bugnyar and Kotschral 2002). However, alternative explanations such as risk-sensitive foraging or differences in the identity of individuals feeding in the different habitats may also have accounted for the observed increased scrounging. Our study provides unambiguous evidence that increasing an individual’s (as opposed to a group’s) vulnerability to predation increases the individual’s preference for the scrounger tactic. However, our experimental design does not enable us to determine whether the antipredator benefits of scrounging are derived from compatibility between scrounging and antipredator vigilance, the spatial position of scroungers within groups, or both. Experiments controlling for the differences in head orientation between tactics are necessary to tease apart these effects.

To date, relatively little is known about the factors influencing interindividual differences in social foraging tactic use (Beauchamp 2000, 2001; Thibautau 2004). We show that individuals adjust their investment in alternative social foraging tactics according to changes in their phenotype, which suggests that interindividual differences in phenotype may also influence individual tactic use decisions. Whereas most studies of producer–scrounger foraging have considered variations in factors at the level of the group, our results demonstrate that the effect of a given factor on tactic use can differ depending on the level at which the factor operates (group or individual). We suggest that phenotype-limited games may be more prevalent than previously suspected, even among groups of similar sized and socially egalitarian individuals.

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