

INTRASPECIFIC COMPETITION INFLUENCES FOOD RETURN-PREDATION RISK TRADE-OFF BY WHITE-CROWNED SPARROWS¹

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Abstract. The trade-off of food return against predation risk was quantified for winter flocking White-crowned Sparrows (*Zonotrichia leucophrys*), and the effect of intraspecific aggression on this trade-off was tested. Feeding bowls, containing a 1-L sand/seed mixture, were placed at three distances from cover. Control treatments (equal seed densities at each bowl) were compared with experimental treatments (higher seed densities farther from cover). More birds fed farther from cover when associated food return was higher, but age-classes responded differently to treatments. On average, dominant adults fed closer to cover than subordinate immatures, even when higher reward was available farther from cover. As predicted if risk of social interaction influences the food return-predation risk trade-off: (1) immatures switched their feeding location more readily than adults and (2) when the reward differential among bowls was especially large, adults shifted to feed farther from cover, and displaced immatures towards the bowl closer to cover. White-crowned Sparrows traded-off food return against predation risk, and this trade-off was influenced by the risk of social interaction such that subordinates were willing to risk higher predation if the risk of social interaction was thereby reduced.

Key words: age, aggression, dominance, food-return, foraging, predation, White-crowned Sparrow, trade-off, *Zonotrichia leucophrys*.

INTRODUCTION

Individuals that forage optimally (Stephens and Krebs 1986) may attempt to maximize their food intake rate. However, individuals also must respond to selection factors which impinge on their ability to maximize this rate. For example, in order to survive to the following breeding season, wintering individuals must not only acquire enough food but also avoid predation. That individuals may trade-off predation risk against food return is well documented in several taxa. For example, Grey squirrels (*Sciurus carolinensis*) decide whether to feed where they are, or move into cover and consume a food item, depending on the size of the food item and the distance from cover (Lima et al. 1985). Sticklebacks (*Gasterosteus aculeatus*) attack smaller prey groups in the presence of a predator because larger groups confuse sticklebacks and thus decrease their chance of detecting a predator (Milinski and Heller 1978). Juvenile wa-

ter-beetles (*Notonecta hoffmanni*) forage at lower prey densities in the presence of adult predators which prey on juveniles (Sih 1982). In addition, individuals may trade-off food return against threat from more than one predator, for example *Gerbillus* spp. forage under bushes in the presence of owls, but in the open in the presence of snakes (Kotler et al. 1993). Furthermore, the trade-off may vary depending on the presence of other prey species, e.g., tits (*Parus* spp.) foraged in less safe locations in a high vole year when Pygmy Owls (*Glaucidium passerinum*) were more likely to catch vole prey (Suhonen 1993). When birds form social foraging flocks, they usually feed as close to cover as possible (Grubb and Greenwald 1982, Schneider 1984, Slotow and Rothstein 1995a). However, when food return close to cover was decreased, individuals foraged farther from cover (Schneider 1984). In such instances, food return and predation risk are traded off against each other (Caraco 1979, Schneider 1984).

Individuals that form foraging flocks face social interference which may affect the balance between food return and predator avoidance. Whereas foraging in flocks may reduce predation risk to any one individual (Hamilton 1971), increased intraspecific aggression may detract

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from foraging time (Keys and Rothstein 1991). Like White-throated Sparrows *Zonotrichia albicollis* (Schneider 1984), dominant White-crowned Sparrows (*Z. leucophrys*) foraged closer to cover than did subordinates (Slotow and Rothstein 1995a). Note that adult White-crowned Sparrows are dominant to immatures (Keys and Rothstein 1991). Furthermore, locations closer to cover were viewed as "better" because individuals were more willing to fight to feed in such locations as manifest by higher aggression rates closer to cover (Slotow 1996). Subordinates may incorporate the risk of an aggressive interaction into their trade-off between food return and predation risk, that is, subordinates may feed at locations of higher predation risk to avoid higher rates of aggression closer to cover. Because aggressive interactions end the foraging bout of subordinates, but not that of dominants (Keys and Rothstein 1991), subordinates may trade-off food return against predation risk differently from dominants. For example, dominant individuals are free to select any feeding location (Hegner 1985) and have the opportunity to forage in locations less exposed to predators or with higher rates of food return, and to assess the "best" feeding location by watching others already feeding (Templeton and Giraldeau 1995, 1996). Subordinates may be forced to feed in less optimal locations, taking into consideration their likelihood of displacement by dominants when choosing where to feed.

Given equal food return at all distances from cover, dominant adult White-crowned Sparrows feed closer to cover than subordinates (Slotow and Rothstein 1995a). However, if food return was varied such that higher reward was available farther from cover, both dominants and subordinates may shift to feed farther from cover. If subordinates incorporate the risk of being displaced from a location into their trade-off, then they would be willing to move farther from cover for a lower reward than would dominants. Furthermore, if the food return was high enough that dominants preferentially fed farther from cover, subordinates may move to feed closer to cover in order to avoid interactions with dominants at locations of high food return.

Accordingly, from the hypothesis that individuals trade-off food return against predation risk, we tested the following predictions of White-crowned Sparrow behavior under various regimes of food return and predation risk: (1)

When food return is constant at all levels of safety, individuals will forage at the safest site, such that, when food density is constant for different distances from cover, an individual would forage as close to cover as allowed by its respective dominance rank. (2) When food return is highest where safety is lowest (farther from cover), birds will compromise safety by foraging farther from cover, such that, all individuals shift location if a high enough food reward is presented farther from cover. (3) Social interactions impinge on the trade-off such that the rate of food return at which dominant adults are willing to compromise safety is higher than the rate at which subordinate immatures compromise safety, such that, the food level at which a shift farther from cover occurs varies according to social rank. To test these predictions we provided small feeding bowls at different distances from cover (equivalent to Schneider's [1984] patchy distribution), and varied seed density in each bowl relative to other bowls.

METHODS

This study was carried out during the winter of 1991 on West (Devereaux) Campus, University of California, Santa Barbara (UCSB), Santa Barbara County. We performed observations of birds feeding on a 2 m × 6 m concrete slab in a mowed field. For a source of cover, we constructed an artificial shrub (2.5 m high × 1.2 m × 1.2 m) from cut conifer branches. The shrub remained on the west side of the concrete slab throughout the study period. Previous work showed that changing the location of the shrub changed the bird's foraging locations, with birds always feeding closest to the shrub (Slotow and Rothstein 1995a). The birds perceived the shrub as a source of cover and not merely as a perch and would not feed unless the shrub was present.

We provided feeding stations, consisting of transparent hard-plastic bowls (diameter 30 cm; depth 5 cm) at different distances to the east of the shrub. The bowls, which allowed up to 15 individuals to feed at once, were filled with 1 L of fine beach sand, into which we mixed varying amounts of millet seed, thus providing a matrix of seed in sand. Hence, search cost (exposure per unit food return) was inversely proportional to seed density. We provided food in the bowls ad libitum on the day prior to each observation period. The design also incorporated resource depletion, because seed density decreased

through observation sessions as birds consumed seed. We verified that there was indeed higher search costs at lower density bowls by performing a titration experiment. We set out four bowls, two close to cover and two far from cover (one high density [120 g of seed] and the other low density [24 g] at each distance). We measured the seed remaining after nine flock visits by naive birds. We found that the seed consumed at high density bowls was significantly greater than at low density bowls (ANCOVA: $F_{1,35} = 72.4$, $P < 0.001$), but that there was no significant effect of distance from cover on depletion rate ($F_{1,35} = 3.56$, $P = 0.069$). In other words, there is greater search cost at lower density bowls. In addition, at the end of each observation session, we sifted the remaining seed from the sand and weighed it. There was always some depletion of seed. On average 4.4 g of seeds was left in bowls starting with 24 g of seed, and 41.3 g was left in bowls starting with 120 g of seed.

We collected data during 19 observation sessions, from early January 1991 until early March 1991. Observations were made in the morning between 07:30 and 10:00 from a car parked 4 m north of the bowls. This late starting time allowed birds time to feed to overcome their overnight fast. Three bowls were placed at 0.3 m, 0.8 m, and 1.3 m from the outer branches of the shrub. This three-bowl array comprised Treatments 1 and 2. These distances were chosen as they span usual feeding distances from cover for White-crowned Sparrows in coastal California (R. Slotow, pers. observ.). In addition, on average 87.5% of all individuals feeding were on Bowls 1 or 2 in a similarly designed three-bowl experiment (Slotow and Rothstein 1995a). For Treatment 1 (10–25 January), we placed equal densities of seed (24 g L⁻¹ of sand) into each of three bowls. This served as the control for Treatment 2 (26–28 January), with 12 g L⁻¹ of seed in Bowl 1, 24 g L⁻¹ in Bowl 2, and 36 g L⁻¹ in Bowl 3.

We made three changes for Treatments 3 and 4: first, we offered birds a more distinct choice using a two-bowl array, with Bowl 1 at 0.3 m and Bowl 3 at 1.3 m from the shrub (the central Bowl 2 was removed). Secondly, we increased the difference in starting seed densities for the experimental treatment. For Treatment 3 (1–3 February), we began with 24 g L⁻¹ of seed in Bowl 1 (at 0.3 m) and 120 g L⁻¹ of seed in Bowl

3 (at 1.3 m). Treatment 4 (16 February–2 March) served as the control treatment for Treatment 3, with 24 g L⁻¹ of seed in both bowls. Lastly, since Mourning Doves (*Zenaida macroura*) interfered with White-crowned Sparrows during the first two-bowl observation session (which we discounted), we modified the experimental setup. We excluded Mourning Doves by placing a semi-circular (40-cm diameter) enclosure of 6-cm diameter mesh chicken-wire over each bowl. The smaller White-crowned Sparrows simply flew through the chicken wire. Whenever White-crowned Sparrows flushed from the bowls they went to the artificial shrub, suggesting that they did not perceive the enclosures as cover from predation. The enclosures per se had no effect on feeding distance from cover (no significant difference between three-bowl and two-bowl control treatments, see Results).

We noted the number of adults at each bowl, every minute (one "count") while birds were foraging. We included all birds on the concrete slab. We counted birds not actually in the bowls as being at the bowl nearest to them, and birds halfway between two bowls as at the bowl they faced. The first count of a feeding period was random, initiated according to a preset electronic minute timer.

On occasion, several other species fed with the White-crowned Sparrows. These included House Finches (*Carpodacus mexicanus*), Mourning Doves, and Golden-crowned Sparrows (*Z. atricapilla*). These species were excluded from all analyses because they were present in much lower numbers.

STATISTICAL ANALYSES

This type of design could have suffered the problem of repeated sampling of the same individual, or pseudoreplication (Hurlbert 1984), inflating sample sizes and thus generating artificially low P values. This problem is especially severe when many data are based on few individuals. However, when there are hundreds of individuals involved, as in our study (see below), there is no reason to expect this sampling method to bias results in any particular direction. We addressed this issue in detail in Slotow and Rothstein (1995a), where we provided the following evidence for the independence of each count: (1) The average length of an individual's feeding bout was less than 1 min. (2) A large

amount of movement took place within our 1-min observation intervals. (3) A large number of different individuals used the feeding site. Trapping records indicated a population of at least 400 individuals using our site over a three day period. In addition, there were 42 flock visits over the course of this study (a flock visit comprised the period from when one bird first alighted until the last bird left the foraging substrate). We provide illustrative data using each 1-min count as an observation. However, to reduce the influence of pseudoreplication, we averaged the number of birds of each age-class on each bowl over 5 min. These averaged values were used for most statistical tests, such that each data point was the average of 5 min of foraging.

We created an average feeding distance for each age-class. For each observation we multiplied the number of adults on Bowl 1 by 0.3, the number on Bowl 2 by 0.8, and the number on Bowl 3 by 1.3. During Treatments 3 and 4, the respective numbers were multiplied by 0.3 and 1.3 because the central bowl was removed. We then summed the values for the three (or two) bowls and divided by the total number of adults on the three (or two) bowls. This gave a mean feeding distance from cover for adults at that observation. We performed a similar calculation for immatures. For example, if there were three adults on Bowl 1, two adults on Bowl 2, and two adults on Bowl 3, for that observation adults had a mean foraging distance from cover of $[(3 \times 0.3) + (2 \times 0.8) + (2 \times 1.3)] / (3 + 2 + 2)$, or 0.729 m.

To contrast the effect of treatment and age on the mean foraging distance from cover, we performed a MANOVA with treatment and age as factors. We took the mean feeding distance from cover for adults and immatures at each count, and averaged these over five consecutive 1-min counts (to reduce the impact of pseudoreplication; see above). We then coded these average feeding distances from cover for treatment and age. To assess the impact of treatment regardless of age, we performed an ANOVA of the mean feeding distance of all birds averaged over 5-min intervals (i.e., the mean of adult and immature feeding distance at each observation). In addition, we performed ANOVAs separately for each treatment to contrast the performance of different age-classes within each treatment. We used Scheffé tests for ad hoc comparisons

among treatments and among age classes with $\alpha = 0.05$. Data were normally distributed both within age and treatment, and overall.

We investigated the effect of adults on immature feeding distance from cover by contrasting the mean feeding distance from cover of immatures when adults also were feeding, to that when adults were not feeding. For these comparisons we had to use the original 1-min counts as individual samples, because averages over 5 min almost always included some adults foraging. Therefore, for these comparisons each data point was a 1-min count. We made separate comparisons for each treatment using Mann-Whitney *U*-tests because data were not normally distributed.

We assessed the impact of seed depletion on adult and immature behavior under the four treatments by contrasting how they behaved as time elapsed (i.e., as seed was consumed). We calculated the proportion of adults that were feeding on Bowl 1 and the proportion of immatures that were feeding on Bowl 1. We compared behavior of adults and immatures during each observation session by correlating the proportion of each age-class present on Bowl 1, against "count" number through the session, i.e., time elapsed. For this analysis we again used the original 1-min counts. As the behavior of one class may affect the other (see Results), we performed Kendall partial correlations (Siegel and Castellan 1988). This analysis provided a nonparametric partial correlation, and held the proportion of one age-class on Bowl 1 constant so as to reveal the correlation of the other with count number.

RESULTS

EFFECT OF TREATMENT ON FEEDING DISTANCE FROM COVER

We performed a MANOVA of all four treatments simultaneously, and found that both treatment ($F_{3,395} = 99.9$, $P < 0.001$) and age ($F_{1,395} = 64.5$, $P < 0.001$) had a significant effect on the model ($F_{4,395} = 90.0$, $P < 0.001$). Treatment had a significant effect on the mean feeding distance from cover regardless of age (mean feeding distance of adults and immatures combined: ANOVA: $F_{3,202} = 60.3$, $P < 0.001$). However, there was no significant difference in feeding distance from cover between the two control treatments (Scheffé test: $P > 0.05$, Fig. 1). This is reassuring and demonstrates that changing

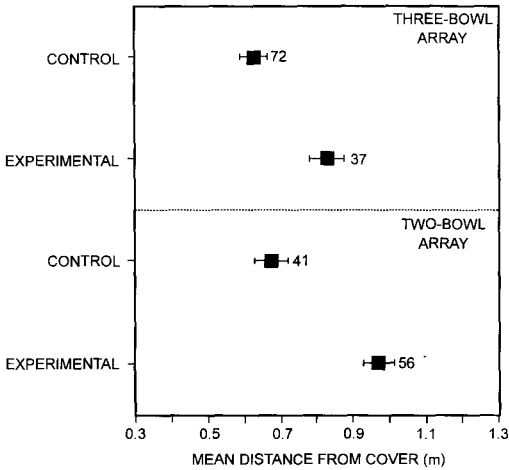


FIGURE 1. The effect of increasing seed density farther from cover on the mean foraging distance from cover of White-crowned Sparrows. Control treatments had equal starting densities at each bowl, and experimental treatments had higher densities farther from cover, and either two or three bowls were arranged at increasing distances from cover. We present the mean feeding distance for each treatment with Scheffé 95% confidence limits (horizontal lines). Sample sizes are averages of five consecutive individual counts.

from three to two bowls, adding dove enclosures, and treatment order had no significant effect on the foraging of sparrows. However, both experimental treatments were significantly different from either of the controls as well as from the other experimental treatment ($P < 0.05$ in all six comparisons, Fig. 1). In other words, regardless of the number of bowls, during control treatments birds fed closer to cover than during the experimental treatments. Increasing the density of seeds farther from cover resulted in individuals shifting their feeding farther from cover (three-bowl experimental treatment, Fig. 1). The effect of further increasing the seed density, and offering only a two bowl choice resulted in birds shifting their feeding even farther from cover (two-bowl experimental treatment, Fig. 1).

DIFFERENCES IN RESPONSE OF AGE-CLASSES TO CHANGING SEED DENSITY

For all treatments, adults had a significantly lower mean feeding distance than immatures (Fig. 2). Note that there were no significant differences in the feeding distance of adults between the two control treatments ($P > 0.05$, Fig. 2). Although more adults still fed on the bowl closest to cover during the three bowl experimental

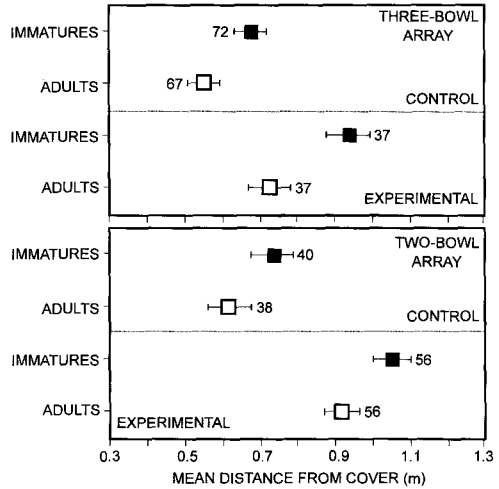


FIGURE 2. The mean foraging distance from cover of immature (filled squares) and adult (open squares) White-crowned Sparrows under different experimental treatments. Control treatments had equal starting densities of seed at each bowl and experimental treatments had higher densities farther from cover (see text). We present means with Scheffé 95 % confidence limits (horizontal lines). Sample sizes are averages of five consecutive individual counts (see text). Within treatment ANOVA's with age as the class variable: three-bowl array control: $F_{1,137} = 21.4, P < 0.001$; experimental: $F_{1,72} = 37.6, P < 0.001$; two bowl array control: $F_{1,76} = 6.69, P = 0.012$; experimental: $F_{1,110} = 12.7, P < 0.001$. See text for other statistical comparisons.

treatment, adults fed significantly farther from cover on average than they did during either control treatment ($P < 0.05$, Fig. 3). During the three-bowl experimental treatment, adults were feeding at the same distance from cover as were immatures under control conditions ($P > 0.05$ in both comparisons). The effect of dramatically increasing seed density farther from cover (two-bowl experimental treatment) resulted in a dramatic shift in adult feeding location such that adults now fed significantly farther from cover than they had in the three-bowl experimental treatment ($P < 0.05$). During the two-bowl experimental treatment, adults fed significantly farther from cover than did immatures under control conditions ($P < 0.05$ in both comparisons, Fig. 2).

The effect of increasing seed density farther from cover also resulted in immatures moving to feed farther from cover (Fig. 2). During both the three-bowl and the two-bowl experimental treatments, immatures fed significantly farther

from cover than during either of the control treatments ($P < 0.05$ in four comparisons, Fig. 2). Again there was no significant difference between the feeding distance of immatures during the two control treatments ($P < 0.05$), nor during the two experimental treatments ($P > 0.05$), although immatures did tend to feed farther from cover during the two-bowl than during the three-bowl experimental treatment. This implies that immatures responded almost completely to the three-bowl experimental treatment and that increasing differences in seed density did not have additional influence on their feeding.

In summary, increasing seed density resulted in both adults and immatures increasing their feeding distance from cover. However, immatures more readily modified their feeding distance from cover than did adults, in that they were more prepared to feed farther out from cover when only a small increase in seed density was made. Adults required a much larger bribe before moving out from cover, but increasing the bribe did not result in further change in behavior of immatures.

EFFECT OF ADULTS ON IMMATURES

For all treatments we compared the mean feeding distance from cover of immatures in the presence versus absence of adults feeding on the bowls. Immatures fed significantly farther from cover when adults were present than when adults were absent in both control treatments (Fig. 3). Similarly, immatures fed significantly farther from cover in the presence of adults in the three-bowl experimental treatment (Fig. 3). However, there was no significant difference in the distance from cover at which immatures fed in the presence versus absence of adults in the two-bowl experimental treatment (Fig. 3).

WITHIN OBSERVATION SESSION AGE-CLASS DIFFERENCES

If age classes differ in their willingness to change feeding location, we expected that as seed was depleted through a feeding session, more individuals would move farther from cover where depletion rates were lower. To test this, we assessed the relationship between the proportion of an age class feeding on the bowl closest to cover, with the time elapsed during an observation session.

For five out of six sessions during the three-bowl control treatment and three out of three

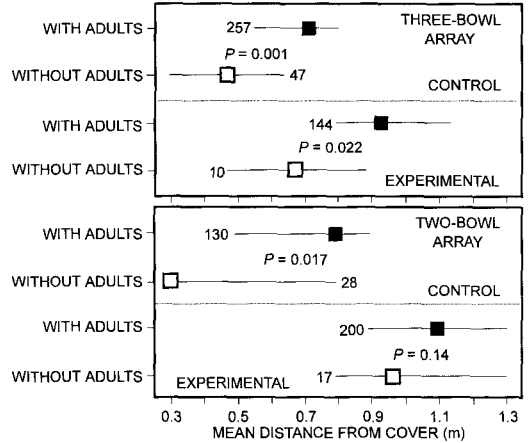


FIGURE 3. The effect of adult White-crowned Sparrows on the feeding location of immatures. We contrast the mean feeding distance from cover of immatures at each observation when immatures were feeding and when adults were present (filled squares), with those observations when adults were absent (open squares). We present the median value with the horizontal lines indicating the first and third quartiles of each distribution. n = number of 1-min counts, P values are for Mann-Whitney U -tests within each treatment between observations with and without adults.

sessions during the two-bowl control treatment, there were no significant correlations between the time elapsed in the observation session and the proportion of the adults present that were feeding on Bowl 1 (Table 1). Indeed, four out of nine correlations were positive for the control treatments, such that, the proportion of adults closer to cover tended to increase as the session progressed. All of the correlations were negative for the experimental treatments (Table 1). In two of three sessions during the three-bowl experimental treatment, and four of four sessions during the two-bowl experimental treatment, there was a significant negative correlation between time elapsed in the session and the proportion of adults present that were feeding on Bowl 1 (Table 1). Therefore during control treatments, adults did not respond to food depletion by moving farther from cover. By contrast, when seed density was higher farther from cover, adults initially fed close to cover and then shifted farther out as the observation session progressed.

For immatures, only one session in the control treatments showed a significant negative correlation between time elapsed and the proportion of immatures on Bowl 1 (Table 1). Unlike adults, there was a consistent trend for the pro-

TABLE 1. The effect of diminishing seed density through a session on adult and immature White-crowned Sparrow behavior.

Treatment	Ses- sion	Adults $T_{xy,z}$ ^a	Immatures $T_{xy,z}$ ^b
Three-bowl control	1	-0.013	-0.058
	2	-0.216	-0.020
	3	-0.048	-0.302*
	4	0.139	-0.077
	5	0.146	-0.021
	6	-0.274*	-0.082
Two-bowl control	1	0.131	-0.425*
	2	-0.128	-0.078
	3	0.134	-0.032
Three-bowl experimental	1	-0.339*	-0.247*
	2	-0.365*	-0.273*
	3	0.031	-0.357*
Two-bowl experimental	1	-0.380*	-0.208*
	2	-0.291*	-0.148
	3	-0.315*	-0.306*
	4	-0.506*	-0.367*

^a Kendall partial correlations of the proportion of the total number of adults present that were on Bowl 1 against the observation number through a session (the proportion of immatures present on Bowl 1 was held constant).

^b Kendall partial correlations of the proportion of the total number of immatures present that were on Bowl 1 against the observation number through a session (the proportion of adults present on Bowl 1 was held constant).

* $P < 0.05$.

portion of immatures on Bowl 1 to decrease with time in the control treatments (Table 1). In the experimental sessions, the proportion of the immatures present that were feeding on Bowl 1 was negatively correlated with time elapsed in six of seven sessions, consistent with the results found for adults (Table 1).

Therefore, it appears that adults were less willing than immatures to change their behavior to feed farther from cover as seed density was depleted. However, if the reward differential was high enough, adults were then prepared to move and feed farther from cover.

DISCUSSION

A trade-off of food return against predation risk has been documented in studies of a variety of taxa, but it has been quantified in only one granivorous bird species, the White-throated Sparrow (Schneider 1984). In the present study, White-crowned Sparrows did trade-off some aspect of foraging against predation risk as was apparent in the control treatments, where more adults and immatures fed closer to cover. The trade-off was modified by changing the potential food return farther from

cover; both dominants and subordinates changed to feeding farther from cover when food return was higher there.

In addition to a higher threat from predation, there may be other disadvantages to feeding farther from cover. For example, foraging farther from cover may increase an individual's vigilance for predators (Caraco et al. 1980, Hogstad 1988), thus decreasing food return. However, we found no evidence for increased vigilance with increasing distance from cover for either adult or immature White-crowned Sparrows (Slotow and Rothstein 1995b). Furthermore, we found no evidence for decreased vigilance with increasing flock size. This is not to say that vigilance for predators does not increase with increasing distance from cover. We suggested that the lack of an increase in vigilance with increasing predation risk was a consequence of an increase in vigilance for conspecifics closer to cover (Slotow and Rothstein 1995b). Indeed, aggression rates were higher closer to cover, and individuals may be more wary of conspecifics closer to cover (Slotow 1996). Predation risk may increase with distance from cover, but there was no decrease in food return rate from increased vigilance. Although subordinate immatures were forced to feed farther from cover, and thus experienced heightened predation risk, they did not suffer a lower food return rate than dominants feeding closer to cover (Slotow and Rothstein 1995b). It is possible that individuals were trading-off the probability of an aggressive interaction (which may end a foraging bout for a subordinate) against predation risk, rather than actual food return against predation risk.

Addressing each of our predictions in turn: (1) When food density was constant, individuals foraged as close to cover as allowed by their dominance rank, with dominant adults foraging closer to cover than subordinate immatures. (2) When food return was highest where safety was lowest (farther from cover), birds compromised safety by foraging farther from cover. In other words White-crowned Sparrows did trade-off foraging against predation risk. (3) Social status and interactions did impinge on this trade-off such that the rate of food return at which adults compromise safety was higher than the rate at which immatures compromise safety; thus, the food level at which a shift occurred to foraging

farther from cover varied according to social rank.

These results are essentially what we would expect given that dominant adult individuals can displace subordinate immature individuals from preferred feeding locations (Schneider 1984, Hogstad 1988, Slotow and Rothstein 1995a). Subordinate individuals that feed under continual threat of displacement have to take advantage of any feeding opportunity immediately, before dominant individuals monopolize the resource. Under such circumstances we expect that subordinate individuals would be flexible in their behavior. That subordinates can have a flexible foraging strategy has been demonstrated recently in Crested Tits (*Parus cristatus*) where subordinates only form coherent flocks with dominants when temperatures fall below a certain level (Lens and Dhondt 1992). Dominant individuals on the other hand need not be opportunistic and can first assess the value of a novel location by watching the food return obtained by others foraging at the site without testing that location themselves (Templeton and Giraldeau 1995, 1996). Because they can displace subordinates from any location, dominants may be more conservative, or cautious in behavior. For example, the sequence of return to a feeder after presentation of a predator model was positively correlated with dominance status in tits (De Laet 1985, Hegner 1985, Hogstad 1988). Thus, immature White-crowned Sparrows were willing to compromise safety at a lower level of food return than were adults. Adults may not have needed to compromise safety for access to food because they can simply displace subordinate immatures from preferred feeding locations.

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