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A rank-specific, cost-benefit analysis of single- and mixed-species flocking in the Black-capped Chickadee

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A rank-specific, cost-benefit analysis of single and mixed-species flocking in the Black-capped Chickadee

Director: Dr. Richard L. Hutto

One interesting facet of temperate zone flocking is that many mixed-species foraging aggregations tend to be temporary, with individuals and species sometimes being found with only conspecifics, and other times with both heterospecifics and conspecifics. Variation in food availability, predation risk, and group composition creates a dynamic environment in which it is likely that the costs and benefits of being a social forager of a particular social rank can change dramatically. It is at the level of the individual that foraging groups can react to these changing conditions; therefore, foraging groups should ultimately develop as the result of decisions taken by individuals to minimize individual cost-benefit ratios. I examined the costs and benefits of social foraging in Black-capped Chickadees (*Poecile atricapillus*) in order to examine whether differences in costs and benefits among individuals may help explain facultative mixed-species flocking. I conducted a three-way factorial experiment in which I manipulated flock composition (single vs. mixed-species), food availability, and predation risk in an outdoor aviary using nine different flocks of wild-caught chickadees. Costs and benefits were assessed by measuring vigilance, foraging efficiency, and interference. Dominant and subordinate chickadees had similar costs and benefits across the different levels of food availability and predation risk. However, subordinate chickadees had significantly higher vigilance and displacement costs than the dominant chickadee in the single species treatment, with middle-ranking chickadees showing the highest costs. The mixed-species treatment reduced these costs for subordinate chickadees and increased these costs for the dominant chickadee, resulting in no significant difference in vigilance and interference costs between subordinates and dominants. Thus, the costs of socially foraging in Black-capped Chickadees vary due to flock composition, and the more dominant individuals may incur higher costs than subordinate flockmates under certain conditions. This asymmetry in costs raises the possibility that the facultative nature of rank-structured mixed-species flocks may be due (in part) to a conflict of interest between subordinate and dominant flockmates, wherein subordinates may actively initiate contact with heterospecifics despite a cost disadvantage to the dominant individual.

Acknowledgments

Mullan Road Nursery, Marchie's Nursery, and Caras Nursery each provided many trees and shrubs for the interior of the aviary. This project was funded in part by a grant from the Five Valleys Audubon Society. I would like to thank Chris Templeton and Caleb Putnam for all of their help in catching chickadees in the cold winter weather, the white trash lab for their help in honing my talks, and my committee for sticking with me after a slow start. Special thanks go to Jon Graham for his statistical expertise, and to my friends and family for keeping my head above water through the dark winter months.

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Introduction

There are thought to be two main potential benefits for social foragers: higher foraging efficiency and lowered risk of predation (Pulliam 1973, Monaghan and Metcalfe 1985, Jullien 2000, Overholtzer and Motta 2000). It is traditionally thought that decreases in food availability or increases in predation risk increase the costs of foraging alone, and therefore increase the probability of social foraging (Powell 1974). These benefits are often countered by costs associated with increased competition for resources (Caraco 1979, Janson 1990, Maniscalco et al. 2001).

One of the most commonly cited ways to reduce the costs of aggregation involves grouping with heterospecifics rather than conspecifics (Morse 1977, Barnard and Thompson 1985). Since competition is usually lower among species than within species, costs of association in mixed-species groups are generally assumed to be lower relative to single species aggregations (Morse 1977, Metcalfe 1989). Furthermore, studies have shown that in mixed-species groups predation risk may be reduced due to increases in overall group vigilance (Hutto 1994, Ronald and Redouan 1997) and that foraging benefits may also be increased via local enhancement (Krebs 1973, Poysa 1992, Sasvari and Hegyi 1998), social facilitation (Waite and Grubb 1988, Peres 1992), lower vigilance rates (Sullivan 1984, Carrascal and Moreno 1992), and increased foraging niche breadth (Morse 1970, Valburg 1992).

One interesting facet of temperate zone flocking is that many mixed-species foraging aggregations tend to be temporary, with individuals and species sometimes being found with only conspecifics, and other times with both hetero- and conspecifics (Morse 1970, Barnard and Stephens 1983, Gautier-Hion et al. 1983, Chapman and Chapman 2000). This suggests that the costs and benefits for an individual choosing to forage socially may change frequently as well. Both food availability and predation risk can vary throughout the environment, and this variation has been shown to affect foraging strategies (Caraco 1979, Elgar 1986, Poysa 1992), vigilance (Monaghan and Metcalfe 1985), and group composition (Berner and Grubb 1985, Caraco et al. 1989, Chapman and Chapman 2000) in birds and mammals.

In many foraging aggregations, the distribution of costs and benefits may also differ among individuals due to dominance interactions (Cimprich and Grubb 1985, Janson 1990, Krams 1996, Hall and Fedigan 1997, Pravosudov and Grubb 1999, Hino 2000). Dominance hierarchies are common within foraging groups, and subordinate individuals have been shown to have lower survivorship (Hogstad 1989, Suhonen et al. 1993), lower foraging efficiency (Pravosudov and Grubb 1999, Hino 2000), and more restricted microhabitat choice than dominant groupmates (Schneider 1984, Suhonen 1993, Hall and Fedigan 1997). Due to these rank-specific differences, it is possible that the costs and benefits of social behavior may differ according to an individual's dominance rank. It is important to note that the difference in costs between dominants and subordinates is primarily due to the ability of the dominant individuals to interfere with subordinates. Thus, the costs for subordinates should be higher only in situations that favor interference by dominants. Furthermore, subordinate flocking behaviours should take advantage of temporally and spatially fluctuating factors that could potentially reduce the level of dominant interference to keep their cost-benefit ratio as low as possible.

Thus, variation in food availability, predation risk, and group composition creates a dynamic environment in which it is likely that the costs and benefits of being a social forager of a particular social rank can change dramatically. It is at the level of the individual that foraging groups can react to these changing conditions; therefore, foraging groups should ultimately develop as the result of decisions taken by individuals to minimize individual cost-benefit ratios (Ekman 1989).

One species that could serve as a good model for investigating social foraging behavior is the Black-capped Chickadee (*Poecile atricapillus*). Chickadee flocks form at the beginning of the winter nonbreeding season and are usually composed of 3-5 pairs of birds. These flocks have been shown to maintain stable dominance hierarchies throughout the winter (Smith 1976), and research has suggested that the costs to subordinate chickadees are much higher than those of dominant chickadees (Cimprich and Grubb 1994, Pravosudov and Grubb 1999).

In addition to flocking in stable groups of conspecifics during the winter, chickadee flocks can also be found in the company of heterospecifics (most commonly Red-breasted Nuthatches (*Sitta canadensis*), but also kinglets, creepers, and woodpeckers) (Glase 1973; pers. obs.). The structure of these mixed-species flocks is very fluid, and the presence or absence of species within the flock is thought to reflect the movements of the core group of chickadees (the "nuclear species" sensu Hutto 1994) through the territories of the other "attendant" species. Although mixed-species flocking in chickadees and their allies (*Parus* spp.) tends to occur more often under conditions of low food availability (Waite and Grubb 1985), high predation risk (Szekaly et al. 1989), and inclement weather (Dolby and Grubb 1999), there has been little progress in uncovering a mechanism that might explain why chickadees are sometimes found in flocks of only conspecifics, while at other times the very same flock of chickadees are found with heterospecifics ("facultative mixed-species flocking" sensu Jullien and Clobert 2000).

This study examined the phenomenon of facultative mixed-species flocking in Black-capped Chickadees from a cost-benefit perspective. I predicted that a pattern of facultative flocking might be due to changes in the costs and benefits of flocking for differently ranked individuals across a range of food availability and predation risk. I also investigated the role of social rank to determine whether subordinates and dominants received the same costs and benefits across the differing conditions of food availability, predation risk, and flock composition.

Methods

Animals

This study was conducted from late December 2000 through March 2001 at the University of Montana's Field Research Station at Fort Missoula (FRS-FM) in Missoula, MT. A total of 9 groups of 6 Black-capped Chickadees (1 group/week) were mistnetted at different locations across the Missoula Valley and were introduced into a large outdoor aviary (16m x 6m x 4m) at FRS-FM. In an effort to make the aviary environment as natural as possible, I furnished the interior with coniferous and deciduous trees, standing dead wood, and a variety of perches on the aviary netting (ca. 1.2 trees/m^2). I supplied sunflower seeds *ad libitum*, and supplemented their diet with a daily ration of mealworms (ca. 6/bird).

One pair of Red-breasted Nuthatches (male and female) were mistnetted in late December to use in the flock composition treatment (see below). Red-breasted nuthatches are interspecifically dominant to chickadees, and are the most commonly observed mixed-species flockmate (pers. obs.). When not participating in the aviary experiments they were kept in an indoor aviary (3m x 2m x 3m) where temperature and light cycle were kept as near to the natural (outdoor) conditions as possible. Nuthatches received mealworms and sunflower seeds *ad libitum.*

Dominance Hierarchies

During the first three days after the capture of each flock, I conducted observations to delineate the dominance hierarchy. I recorded the outcome of every displacement and aggressive interaction and scored each bird as a winner or loser. Rank was determined from these interactions using a win-loss matrix (sensu Pravosudov and Grubb 1999). The rank of an individual is stable throughout the winter (Smith 1976), and there were no changes of rank within any of the flocks during the experiments.

Aviary Experimental Design

In order to investigate the potential roles that food availability, perceived predation risk, and flock composition play in determining the relative foraging costs and benefits of different ranking birds, I designed a three-way factorial experiment to test the effects of each of these factors and their interactions. Food availability was manipulated at two levels: a centralized treatment, with one, single-opening feeder (1 feeder/6 chickadees), and a dispersed treatment with six feeders (1 feeder/1 chickadee). I influenced the perceived predation risk by playing "high zee" chickadee alarm calls (used primarily for high risk aerial predators (C. Templeton, unpublished data)) for 15-20 s at the beginning of the increased predation treatment. Finally, I altered the flock composition within the aviary by adding a pair of Red-breasted Nuthatches for the mixed-species treatment, and removing them for the single-species treatment.

To tease apart rank-based differences in response, I used focal observations on three different birds: the most dominant bird (rank 1, "dominant"), the middle subordinate bird (rank 3, "middle") and the lowest subordinate bird (rank 6, "subordinate"). This approach allowed me to look for differences not only between the dominant and the two subordinates, but also between the two differently ranked subordinates. Each experiment included four days of focal observations on each of the three ranks (Figure 1). Observations began a half-hour after sunrise and consisted of twelve 20-minute trials. In order to control for variation induced by the progress of the day, I assigned 6 trials to an early morning block and 6 to a late morning block, and within each block I randomized the order in which ranks were observed. I also recorded the temperature at the start of each trial to control for the effect of environmental fluctuations. The flock and food treatments were randomized across the four days, and the predation treatment was randomized across the six trials in each block. Thus, each focal rank was observed twice in each block, once with increased predation risk and once without, for a total (at the end of each experiment) of four observations/focal rank/treatment combination (food x flock x predation). I then replicated this experiment using 9 different groups of chickadees.

Response Variables

The response variables were chosen to determine the relative foraging benefits of individuals in different treatments, and to look at the potential costs incurred in each treatment. I assessed the foraging benefits using three measures: (1) food consumption rate (seeds eaten/min); (2) the average handling time per seed; and (3) the proportion of seeds eaten (seeds eaten/seeds acquired). I assumed that higher consumption rates, lower average handling times, and a higher percentage of seeds eaten reflected overall higher foraging benefits. Indirect interference costs were measured by looking at the proportion of seeds lost relative to the number of seeds eaten (seeds lost/seeds eaten). The loss of a seed during handling is a common outcome of avoiding dominance-related interference (pers. obs.), and I assumed that higher proportions of seeds lost relative to eaten reflected an indirect cost of foraging socially.

I also examined foraging tradeoffs by recording the vigilance rate while eating (scans/s). In order for a chickadee to consume a sunflower seed, it must hold the seed in its feet while perched in order to both peck at the hard covering and to extract the flesh of the seed. I considered a bird to be scanning if its bill was raised above the horizontal position

(Pravosudov and Grubb 1999). Since this type of vigilance behavior is mutually exclusive from ingesting food, it represents a measure of time that could have been spent on another behavior (i.e. resting, eating, etc). For these reasons I assumed that increased vigilance was a costly behavior.

Finally, I measured direct interference costs between birds by recording displacements. I scored an interaction as a displacement if an individual was supplanted from a perch by another individual. This type of interaction represented the cost of direct interference.

Statistical Tests

I used univariate mixed-model ANOVAs to examine the treatment effects on each response variable. The food, predation, and flock treatments were used as fixed factors along with the focal rank. I integrated the block effect and the week of each experiment as random factors, and included the time of day (relative to sunrise) and temperature as covariates in the model. The model consisted of each of the main effects and all of the interactions between focal rank and the fixed factors. Due to problems regarding variance homogeneity, the displacement data were analyzed separately using chi-square goodness-of-fit tests.

I also employed a varimax-rotated principal components analysis (PCA) with all of the response variables included as factors in order to examine the similarity in overall costs and benefits among focal ranks.

Results

Food and predation treatment

The interaction of rank with both the food and predation treatments had little effect on the response variables that I measured (Table I). The only variable that changed significantly due to these treatments was the percent of seeds eaten. The dominant rank decreased its percent eaten when predation risk was increased (Figure 2), and the most subordinate rank increased its percent eaten when food was dispersed in the aviary environment (Figure 3). In all other respects there were no differences between the different ranks across the different food and predation risk factors in the ANOVA analysis.

The middle and lowest ranked birds in each flock were displaced more often than the dominant rank in the centralized food treatment and in the dispersed food treatment, and the middle rank was displaced the most (Figure 4). The middle rank was also displaced more often under increased predation pressure, and carried the highest proportion of displacements (Figure 5).

Flock Treatment

In contrast to the food and predation treatments, the interaction between rank and the flock treatment affected nearly every variable significantly (Table I). During the single species treatment there was no difference in food consumption among ranks (Figure 6), but there was a trend towards higher costs in more subordinate individuals (Figures 7-10). In general, the most subordinate rank exhibited significantly higher average handling times than both the middle and the dominant rank (Figure 7), and lost a greater proportion of seeds when compared to the most dominant rank (Figure 8). However, for vigilance behavior, the middle rank scanned significantly more often than either the dominant rank or the most subordinate rank (Figure 9). The middle rank also shouldered a greater proportion of the displacements than the subordinate (Figure 10).

The mixed-species treatment resulted in a general trend towards reduced costs and higher benefits; however, these trends were seen only for the middle and subordinate ranks. The subordinate rank consumed significantly more seeds than in the single species treatment, and both the subordinate and the middle rank consumed significantly more seeds than the dominant rank in the mixed-species treatment (Figure 6). Although the proportion of seeds lost was equal across ranks, the subordinate rank lost significantly less when nuthatches were present (Figure 7). Furthermore, average handling times and vigilance behaviour decreased significantly for both the middle and subordinate ranks (Figures 8-9). Vigilance increased significantly, however, for the dominant rank and was significantly higher than both the middle and subordinate ranks (Figure 9). The number of displacements also increased significantly for the dominant rank and decreased significantly for the middle rank, resulting in no difference in the distribution of displacements across ranks (Figure 10).

Principal Components Analysis

Most of the factors were organized along the two primary axes, which described a combined 72.6 % of the variation in the data. Because the proportion of seeds lost was not strongly associated with either of the two axes, the PCA was re-run without them (Table II). Higher consumption rates and percentage eaten were positively associated with principal components axis 1 (PC1), and higher average handling times were negatively associated with PC1 (Table II). Thus, as values increase along PC1, benefits (consumption rate, percentage eaten, and lower handling times) are increasing as well. Increased vigilance and higher displacements were positively associated with principal components axis 2 (PC2) (Table II). Therefore, higher values along PC2 indicate higher costs (Figures 11-12).

Flock treatment

All three ranks were significantly different from each other during the single-species treatment. The combined costs (PC2) for the most subordinate rank were significantly lower than for the middle rank with the middle rank carrying the highest costs and the dominant rank displaying the lowest costs (Figure 11). Variance in combined costs (indicated by the vertical width of the ellipses) was highest for the middle rank and lowest for the dominant. In contrast, there were no significant differences in the combined benefits accrued by the three ranks; however, the most subordinate rank showed the greatest variation in benefits (Figure 11).

In the mixed-species treatment, all three ranks became more similar to each other, and there were no significant differences in the relative combined costs and benefits for any of the three ranks (Figure 12). Subordinates again exhibited the greatest variation in benefits, but variance in costs was equal across ranks (Figure 12).

Discussion

This study establishes that the costs and benefits of socially foraging can differ not only due to an individual's social rank, but also due to the interaction of an individual's rank with the availability of food, perceived predation risk, and flock composition. Although the food and predation treatments only marginally affected the costs and benefits for each of the three ranks, the flock treatment significantly affected nearly all of the variables. Mixed-species flocking generally increased the benefits for subordinates while also decreasing their costs. In contrast, the dominant rank tended to have higher vigilance and displacement costs when nuthatches were present. Thus the mixed-species treatment had a homogenizing effect on the combined cost-benefit relationship.

My results suggest that the relative cost of being a subordinate may, in fact, be much lower than previously estimated. Many earlier studies have come to the conclusion that subordination is very costly (Ficken et al. 1990, Daily and Ehrlich 1994, Lahti 1997), and although in my study subordinates in single-species flocks did have higher costs than in mixed-species flocks, these costs were unaltered by changes in food availability or perceived predation risk. One explanation for these lower costs involves the aviary in which the experiments were conducted. In contrast with many experimental flocking studies which used small simplified aviaries and flocks (e.g. Pravosudov and Grubb 1999), my aviary was large enough to accommodate a flock of birds at biologically realistic densities. Furthermore, the environment within the aviary contained many trees, perches, and potential refugia for subordinates that closely mimicked the natural environment. This increase in structural complexity and space probably resulted in less interference from dominant flockmates than has previously been reported (Alatalo et al. 1986).

While this study suggests that the costs of being a subordinate may not be as high as previously thought, it also demonstrates that the relative costliness of being a subordinate may also be strongly influenced by the exact rank of a bird within a dominance hierarchy. This possibility has often been overlooked in studies involving dominance hierarchies, which usually group the subordinates for comparison against the dominant (Hogstad 1989, Suhonen 1993, Daily and Ehrlich 1994).

A lumping approach to dominance and social rank may obscure important biological reality lurking beneath. For example, in my study, both vigilance rate and the proportion of displacements were highest for the middle rank, lower for the most subordinate, and lowest for the dominant rank. If the data were grouped together the subordinate ranks would still have had higher costs than the dominant (unpublished data), but I would have missed an interesting result: that the middle rank actually carries higher vigilance costs than the lowest rank.

This result probably reflects an important aspect of being a middle-ranked subordinate; if an animal is dominant, it should be vigilant for predators and for opportunities to scrounge from subordinate group members. The middle rank should not only be vigilant for predators and scrounging opportunities, but also for the possibility of being the subject of interference from a dominant individual. This means that middle ranking birds must, in a sense, visually interrogate every bird that approaches to determine its rank and intentions. However, the most subordinate birds do need to determine the rank of an approaching bird because every other flockmate is dominant, and instead of being highly vigilant, they compensate by using more perches while foraging (Eldermire, unpublished data). Thus, taking a closer look at traditional dominant-subordinate relationship in stable membership flocks might reveal a better understanding of the inner workings of flock dynamics.

Although mixed-species flocking has been investigated from the perspective of both the "nuclear" species (Morse 1970, Hutto 1994, Cimprich and Grubb 1994) and the "attendant" species (Dolby and Grubb 1998), few studies have examined it from the perspective of the individual. In general, flock dynamics have been ascribed to the group as a whole; however, my results suggest that subordinate birds (especially middle-ranking birds) may gain the most from foraging with dominant heterospecifics, while dominant birds may have a net loss. This result raises the possibility that subordinate ranks could be initiating mixed-species flocking with dominant heterospecifics in order to reduce the level of intraspecific interference. Traditionally, subordinates have been viewed as little more than cannon fodder exploited by the dominant, forced to forage in the riskiest areas (Grubb and Greenwald 1982, Suhonen 1993). My results suggest that there may be other options available to subordinate ranks that have not been investigated thoroughly, and provides further evidence that subordinates are not 'herded' by dominants (Ekman and Askenmo 1984).

Recent studies have indicated that there can be intraspecific, dominance-related differences in benefits from mixed-species flocking (Hino 2000); however, my study demonstrates that dominant individuals may actually incur higher foraging and vigilance costs than subordinates (Monaghan and Metcalfe 1985), and that subordinates may be able to influence their own cost-benefit levels by seeking out dominant heterospecifics. The asymmetry in costs and benefits suggests that there may be a conflict of interest between dominant and subordinate ranks regarding their propensity to flock with other species.

This conflict of interest may form the foundation for the facultative basis of mixed-species flocking in Black-capped Chickadees. Middle-subordinate birds form the bulk of the flock, and could potentially dictate the direction in which a flock moved to increase the likelihood of encountering a dominant heterospecific. Although costs for dominant ranking birds may increase in mixed-species flocks, it is likely that the overall costs of his remaining in the flock are lower than foraging alone (Pravosudov and Grubb 1999).

Yet if the dominant's costs were to rise sufficiently to make foraging alone a better option, subordinate birds could potentially suffer. Hogstad (1989) found that subordinate Willow Tits tended to have higher survival in the presence of dominant individuals than when they were removed, and concluded that it was likely that subordinate birds probably gain important information from the presence of dominant individuals. Thus, the temporally and spatially fluctuating pattern of single and mixed- species flocking that is normally encountered may, in part, reflect a tug-of-war between the interests of the dominant and subordinate flock members.

In conclusion, this study demonstrates that the interaction of social rank and flock composition (and to a lesser degree, food availability and perceived predation risk) can have a great influence on the costs and benefits realised by individuals. The asymmetries in costs and benefits among differently ranked individuals reported in this study form the basis for a new perspective on the potentially important role that subordinate individuals may play in manipulating the formation of mixed-species flocks. More detailed studies of rank-specific behaviours and movements across a range of food availability, predation pressure, and flock composition are needed to ascertain the significance of dominance interactions in mediating changes in flocking strategies.

Table I. Univariate ANOVA statistics for each factor interaction and response variable

	rank x flock		rank x food		rank x predation	
response variables	*F*	*p*	*F*	*p*	*F*	*p*
seeds eaten /minute	5.985	0.003**	0.792	0.454	0.092	0.912
seeds eaten /acquired	1.243	0.29	5.145	0.006**	3.17	0.043**
seeds lost/eaten	3.469	0.032**	0.354	0.702	0.503	0.605
avg. handling time	3.762	0.024**	0.542	0.582	0.725	0.485
scans/s	46.747	<0.0001**	1.631	0.197	0.591	0.554

** = significant result

Table II. Principal components analysis factors, extraction scores, and component values for the flocking treatment for two models.

	inclusive model			exclusive model		
PCA factors	extracted	PC1	PC2	extracted	PC1	PC2
percent eaten	0.854	0.907	-0.175	0.902	0.948	-0.006
consumption rate	0.613	0.781	-0.006	0.802	0.891	0.009
avg. handling time	0.432	-0.657	-0.004	0.381	-0.616	-0.003
vigilance	0.737	-0.122	0.850	0.777	-0.156	0.867
displacements	0.785	0.201	0.863	0.771	0.108	0.872
seeds lost	0.009	0.297	0.007	n/a	n/a	n/a

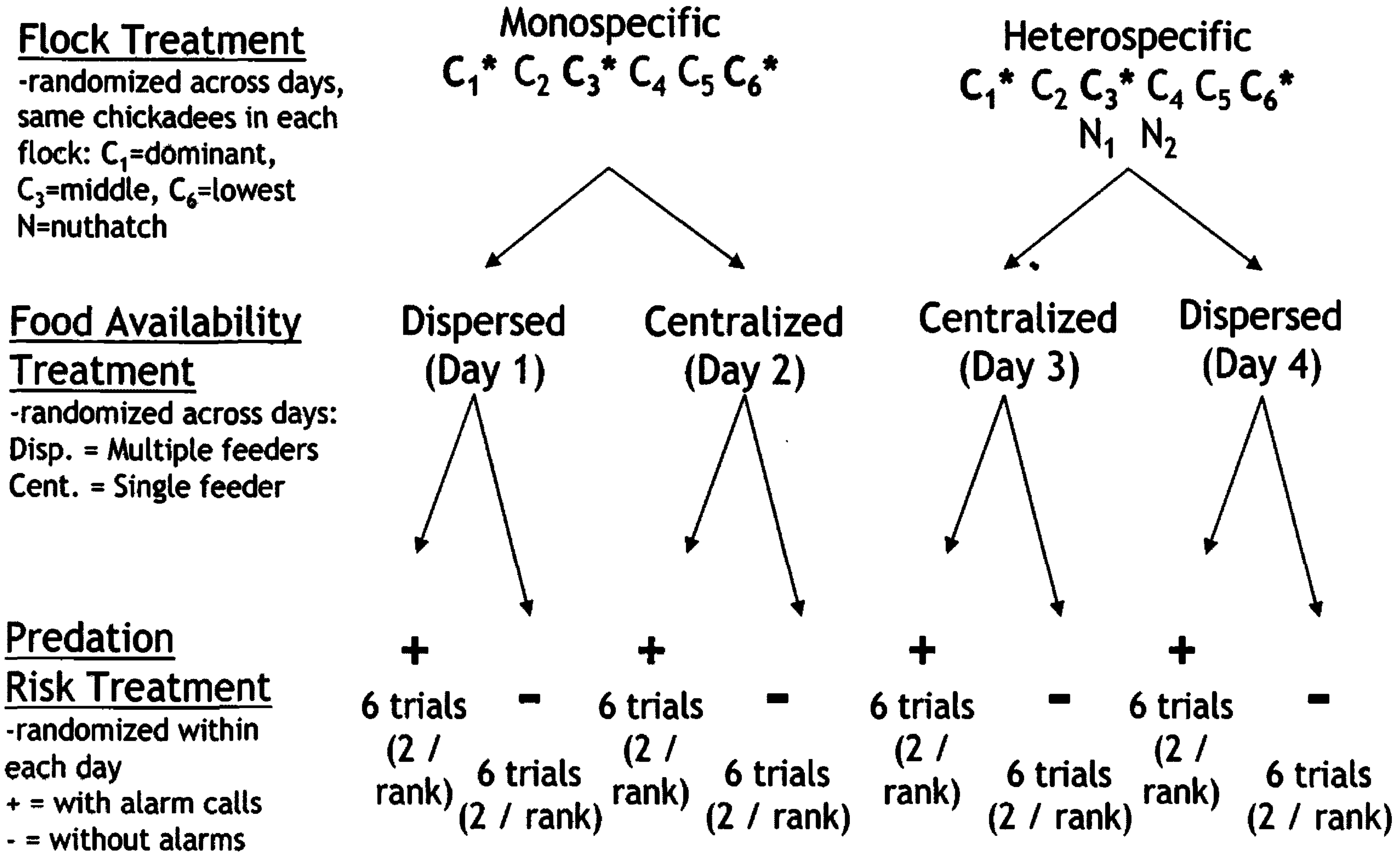

Figure 1. Flowchart detail of the aviary experimental design

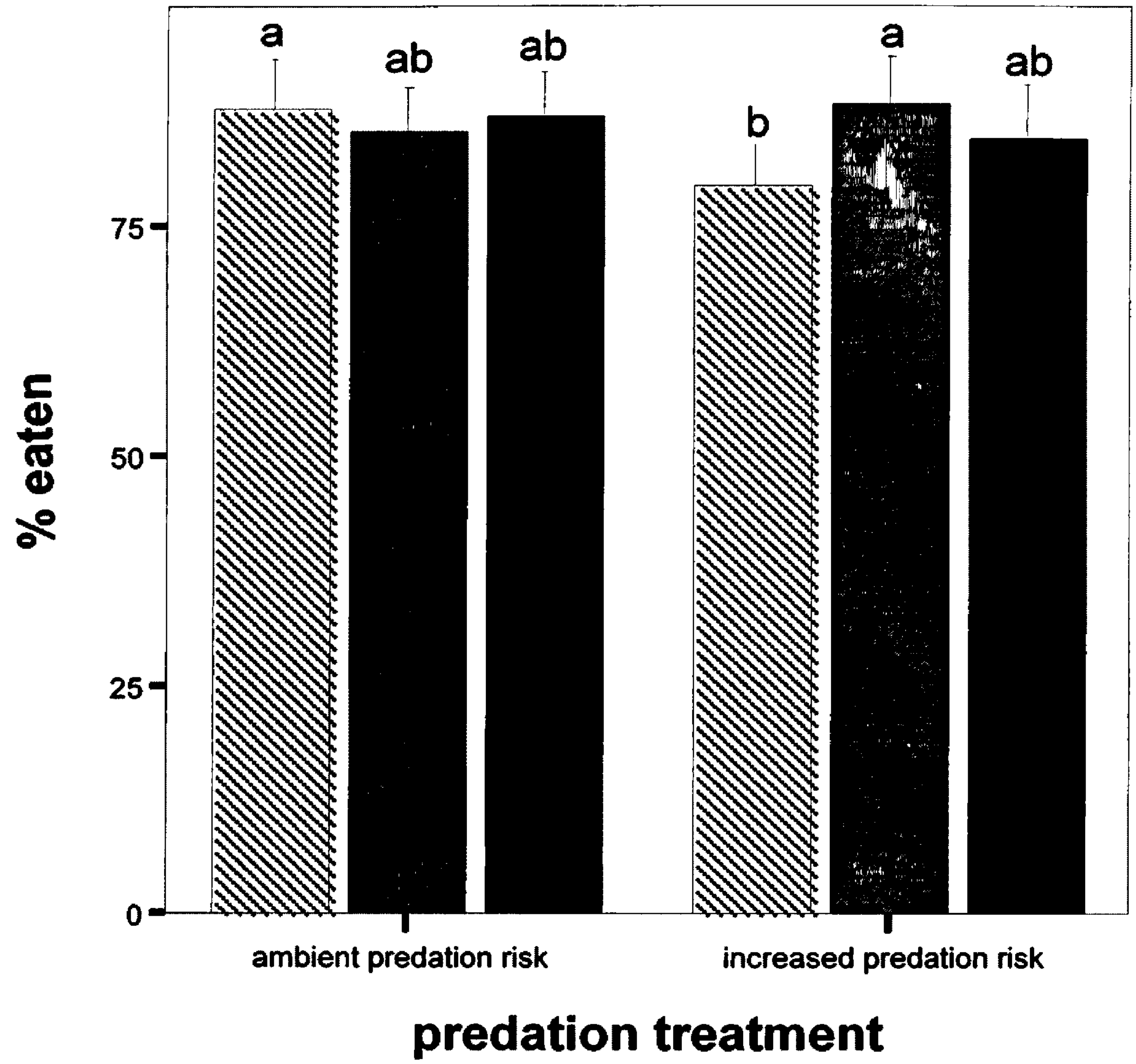

Figure 2. The mean percentage of seeds eaten by each of the ranks across predation treatments. Hatched bars designate the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Error bars represent 95% confidence intervals around the mean.

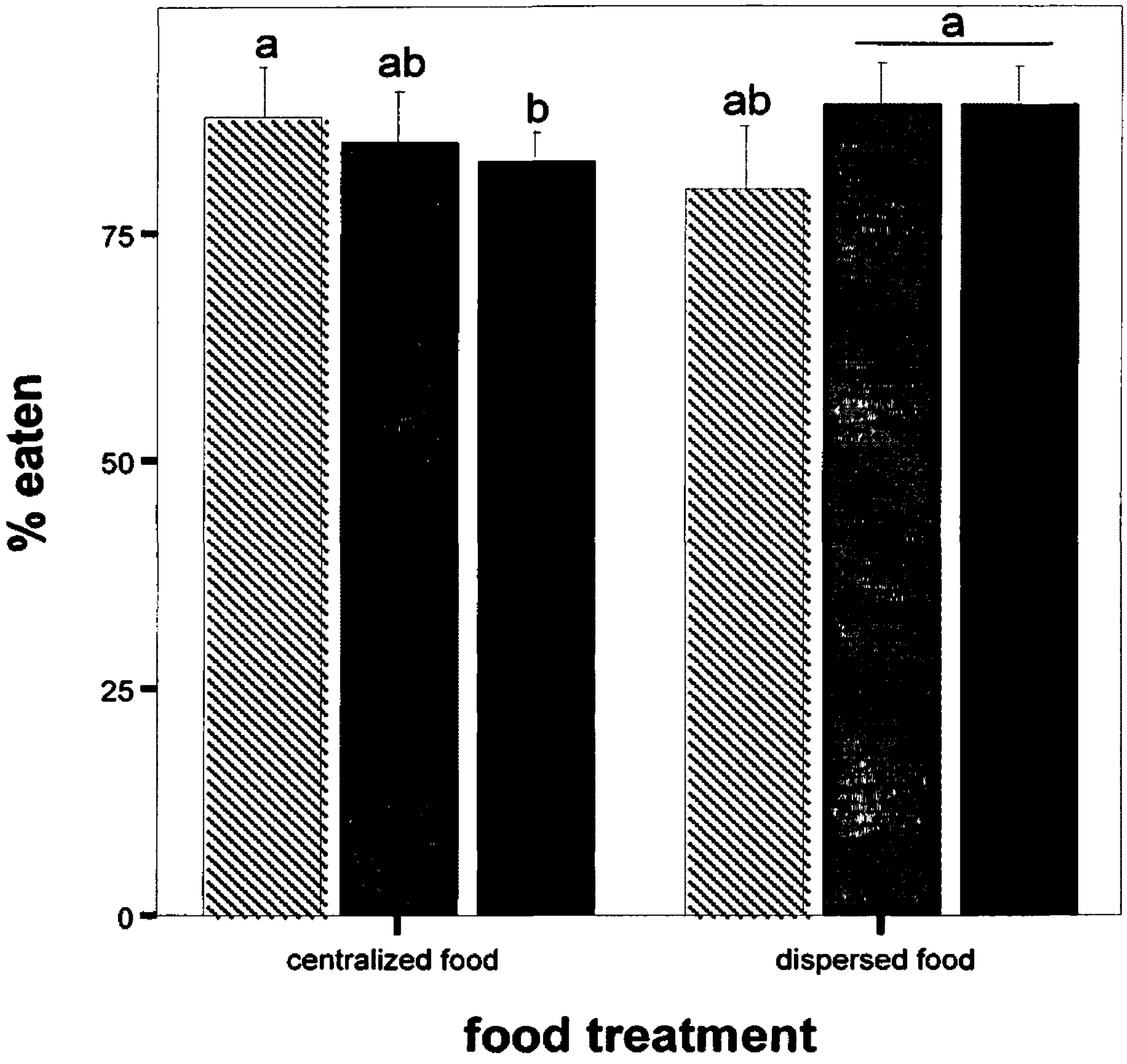

Figure 3. The mean percentage of seeds eaten by each rank across food treatments. Hatched bars designate the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Error bars represent 95% confidence intervals around the mean.

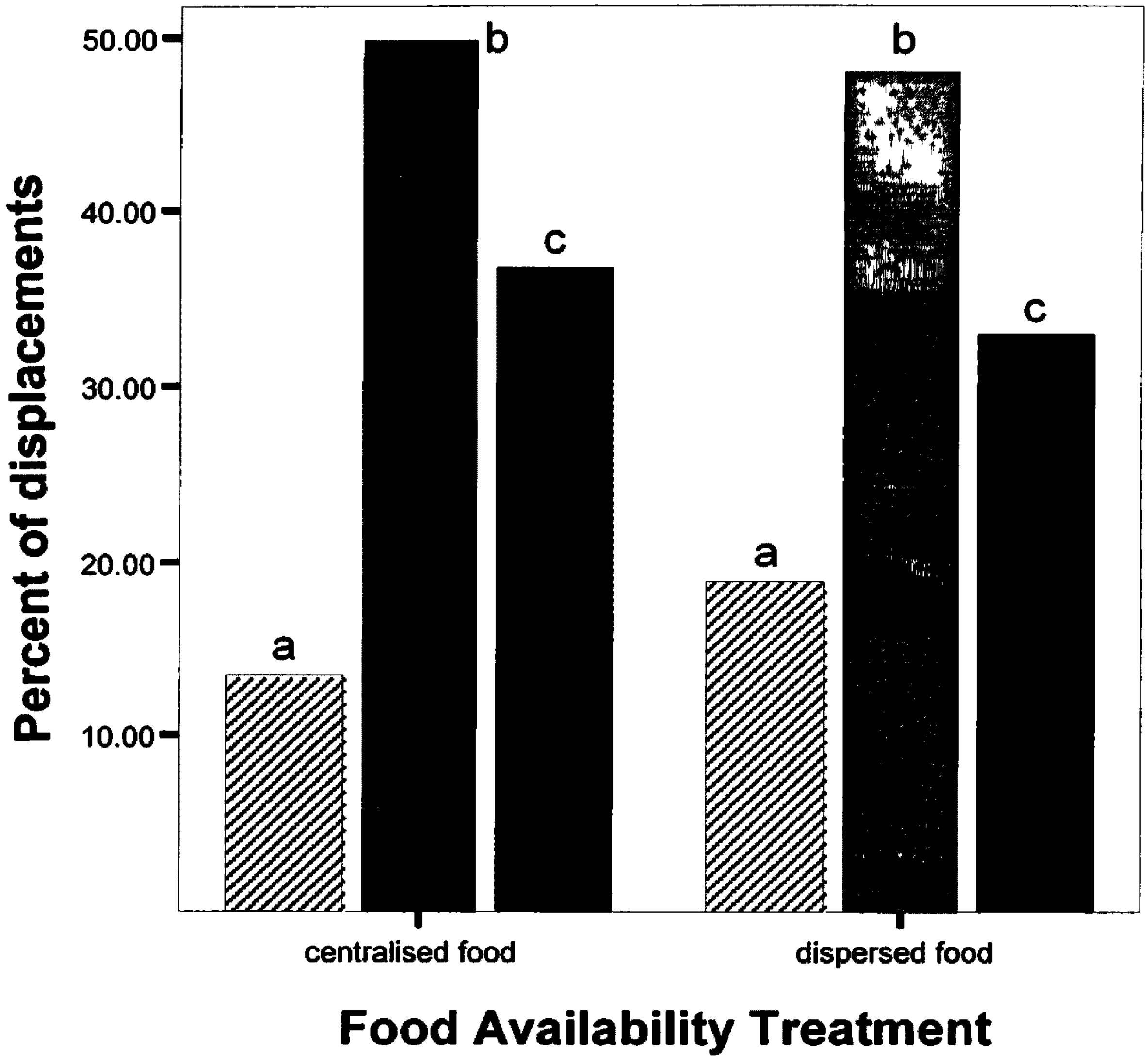

Figure 4. Percent of displacements experienced by each rank across food treatments. Hatched bars designate the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Letters indicate significantly different values (chi-square, $p<0.001$).

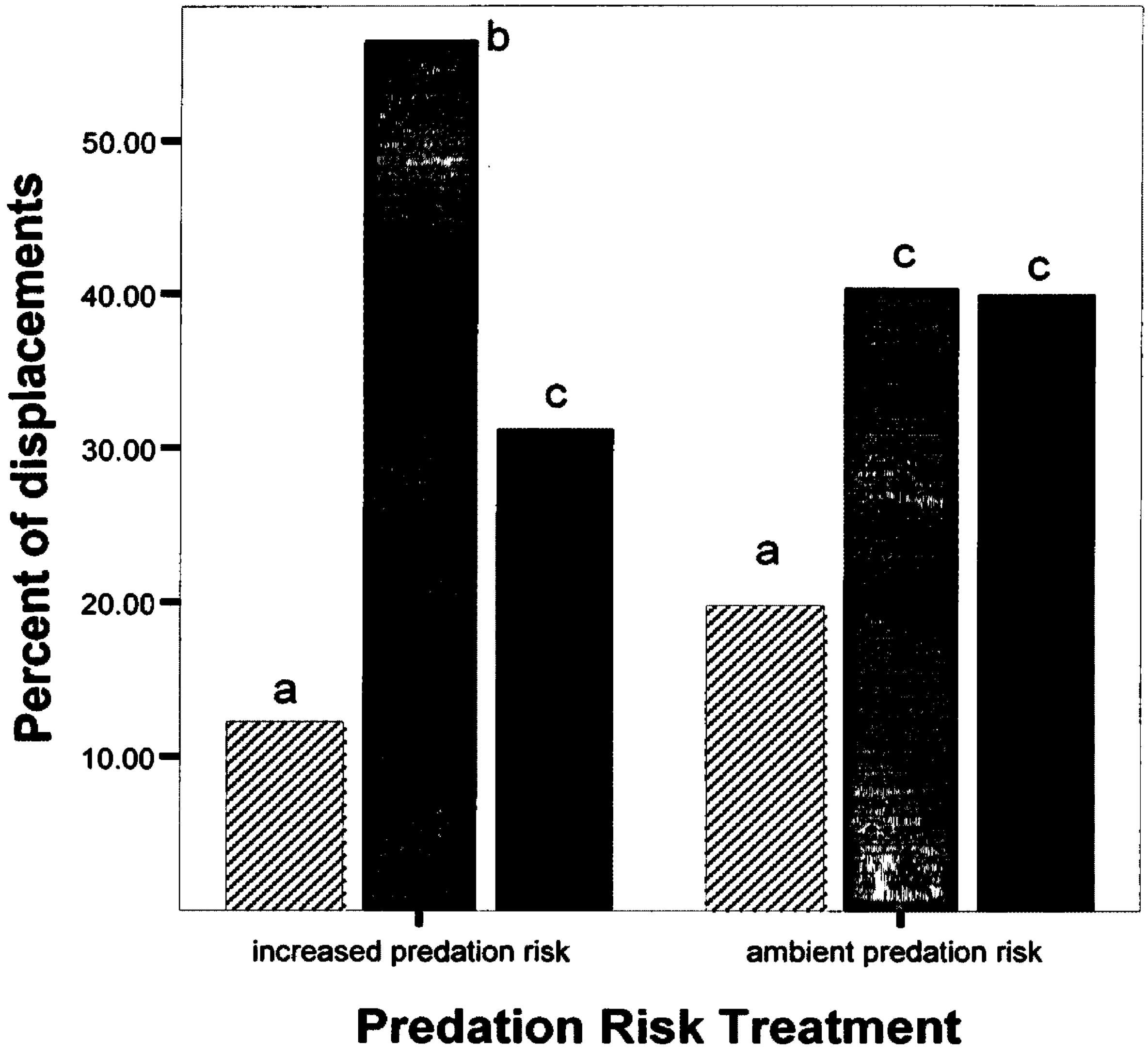

Figure 5. Percent of displacements experienced by each rank across predation treatments. Hatched bars designate the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Letters indicate significantly different values (chi-square, p<0.001).

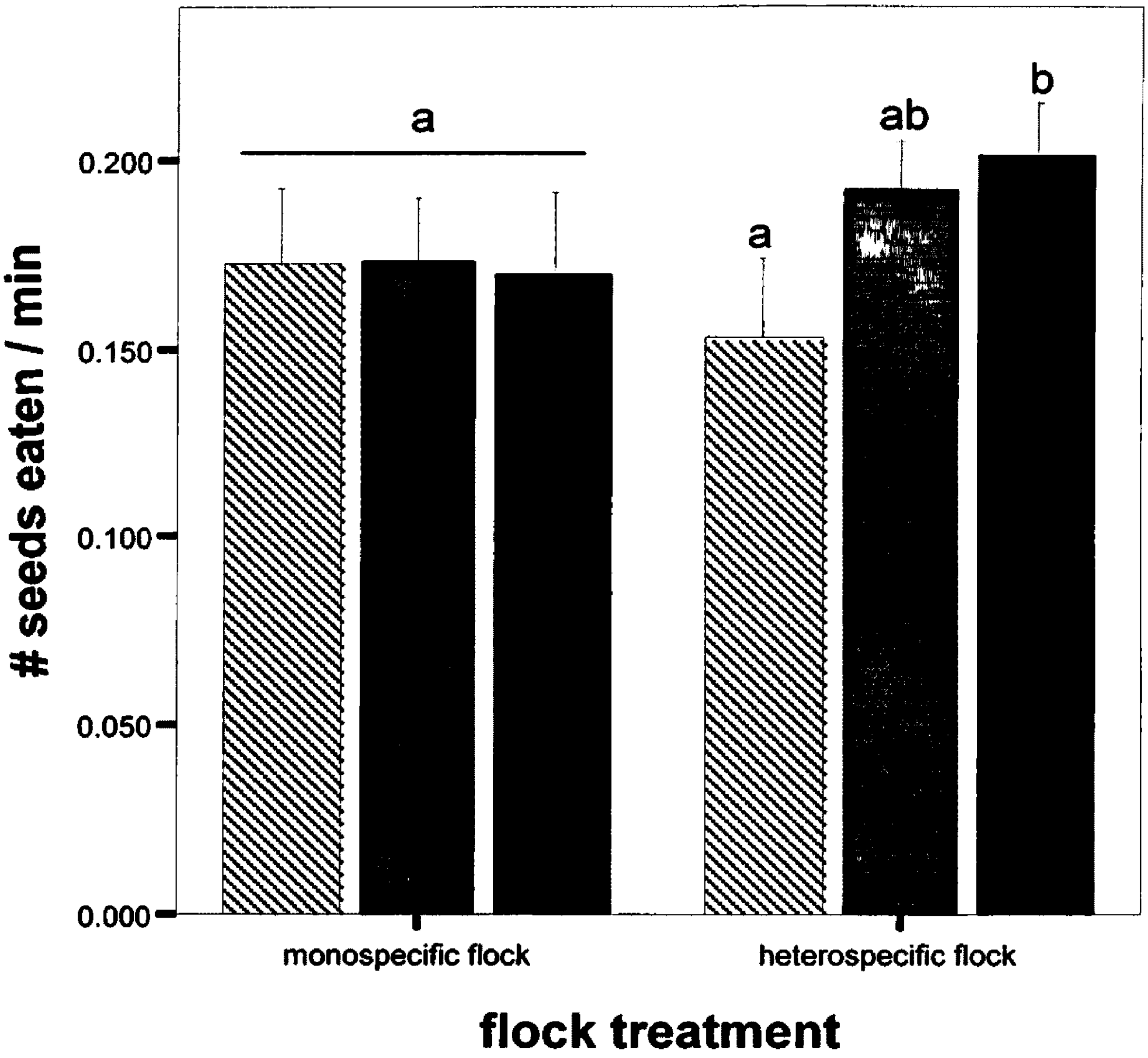

Figure 6. The mean number of seeds eaten / minute for each rank across flock treatments. Hatched bars are the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Error bars represent 95% confidence intervals around the mean.

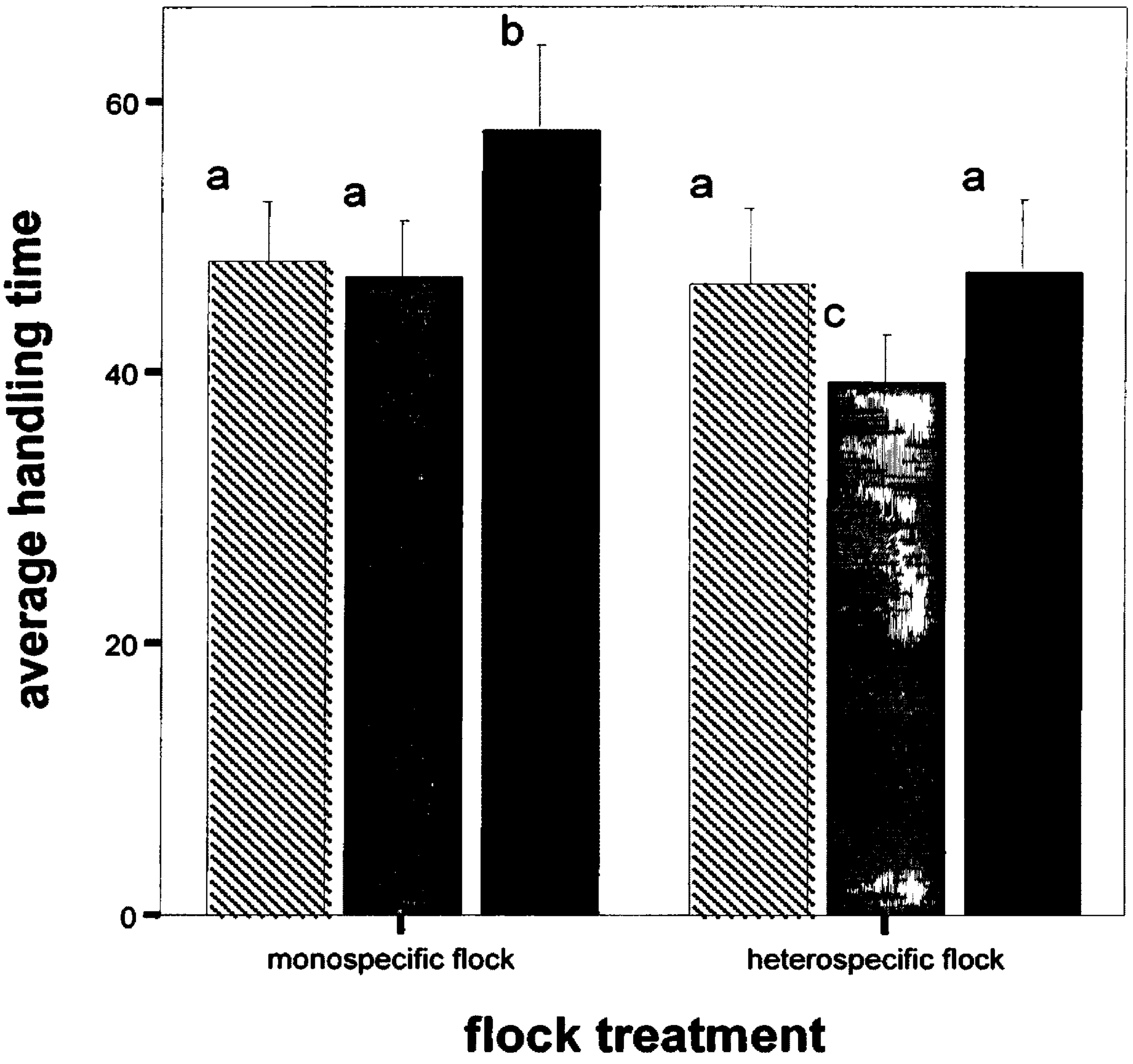

Figure 7. Average handling times (in seconds) for each rank across flock treatments. Hatched bars designate the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Error bars represent 95% confidence intervals around the mean.

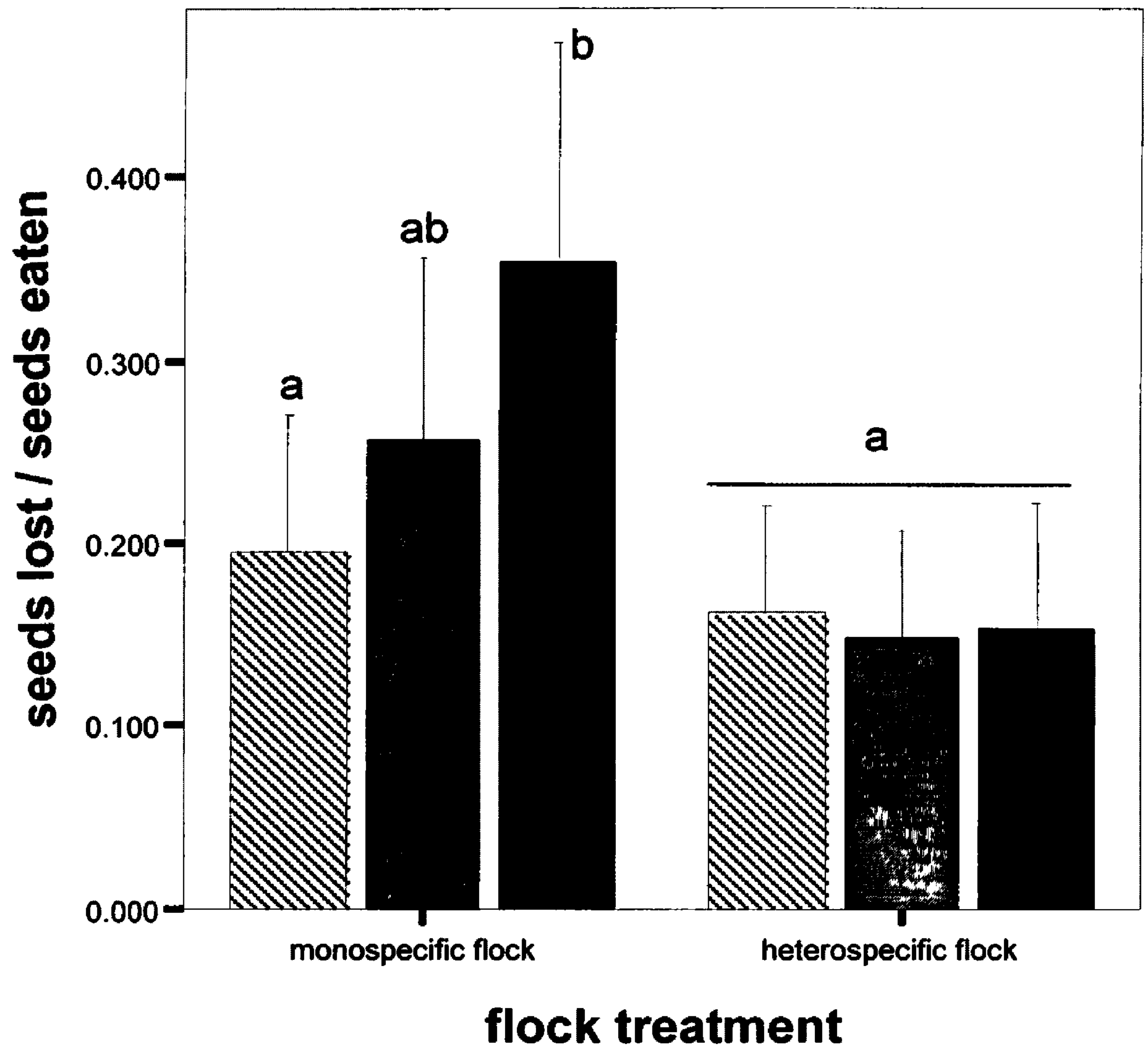

Figure 8. The mean proportion of seeds lost relative to seeds consumed for each rank across flock treatments. Hatched bars are the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Error bars represent 95% confidence intervals around the mean.

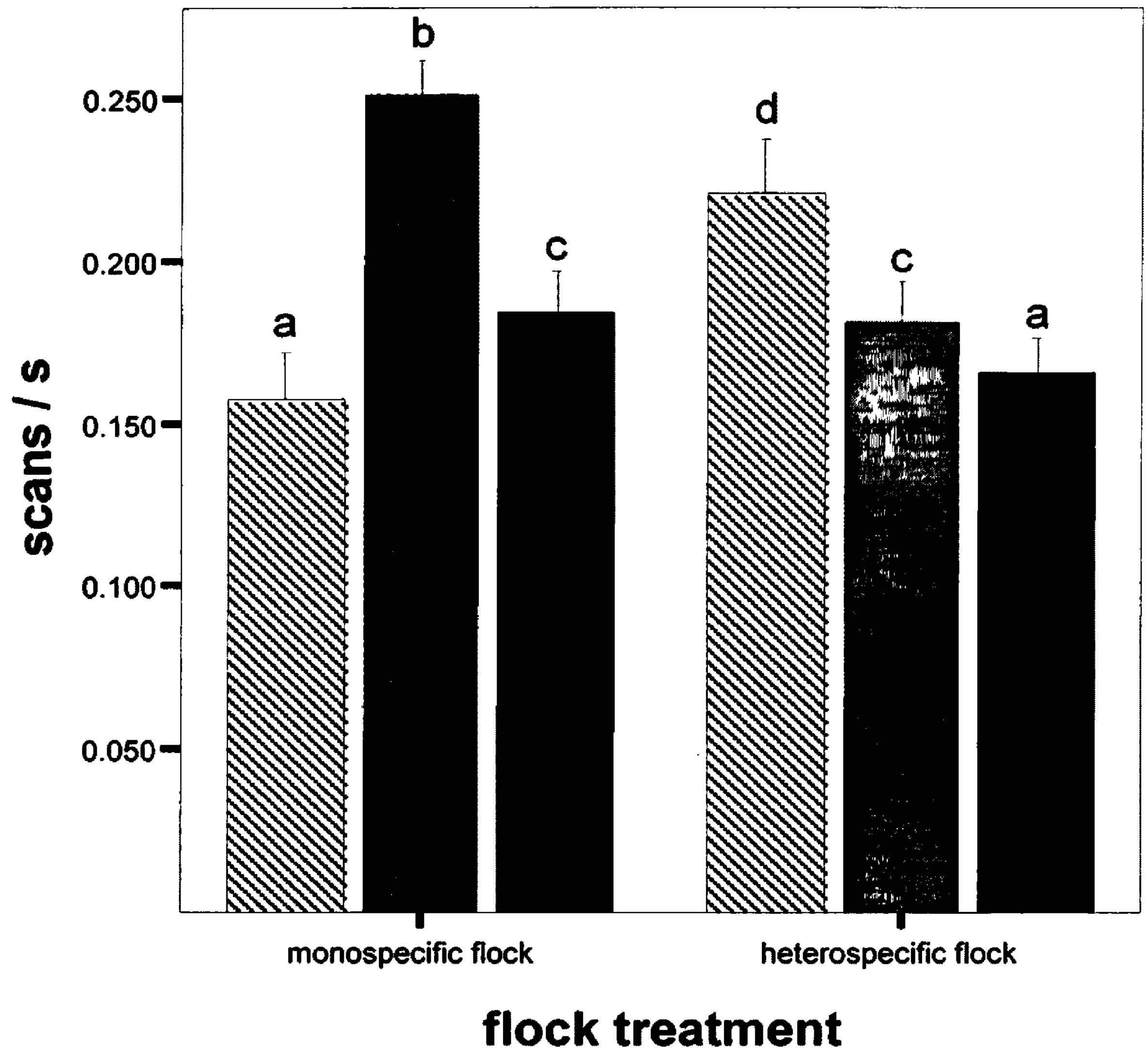

Figure 9. The mean number of scans/s while eating for each rank across flock treatments. Hatched bars designate the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Error bars represent 95% confidence intervals around the mean.

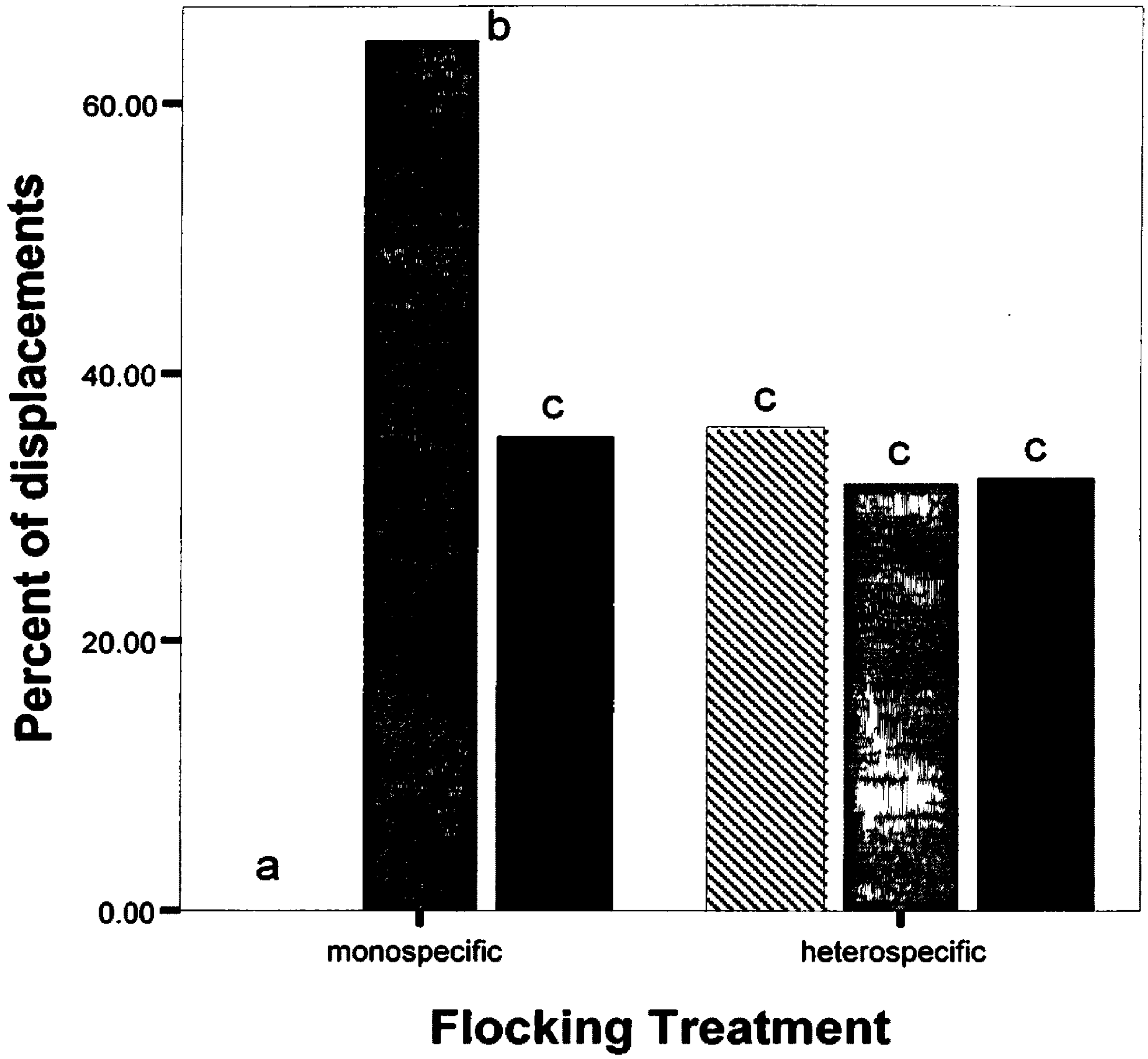

Figure 10. The percent of displacements experienced by each rank across flock treatments. Hatched bars represent the dominant rank, grey bars indicate the middle rank, and black bars indicate the subordinate rank. Letters indicate significantly different values (chi-square, p<0.001)

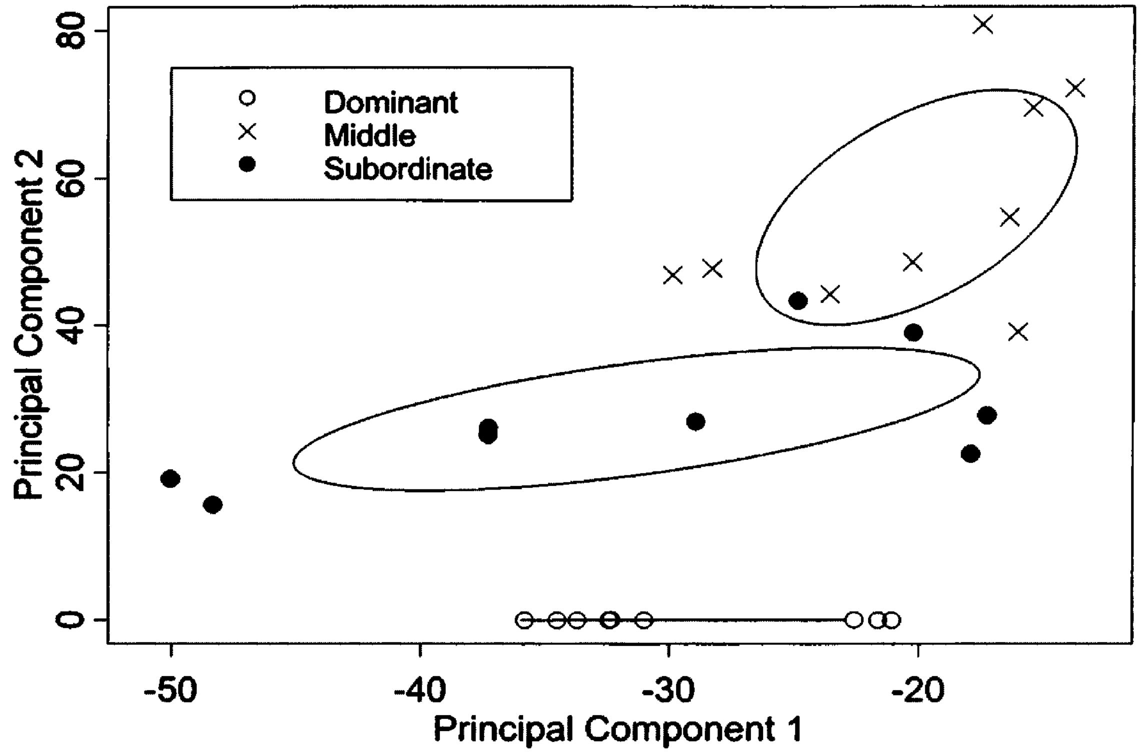

Figure 11. Principal components biplot for single species flock treatment. Costs (i.e. vigilance and displacements) increase along the y-axis (PC2), and benefits (seed consumption, percentage eaten, and lower handling times) increase along the x-axis (PC1). Ellipses represent 95% confidence areas around the centroid of each rank.

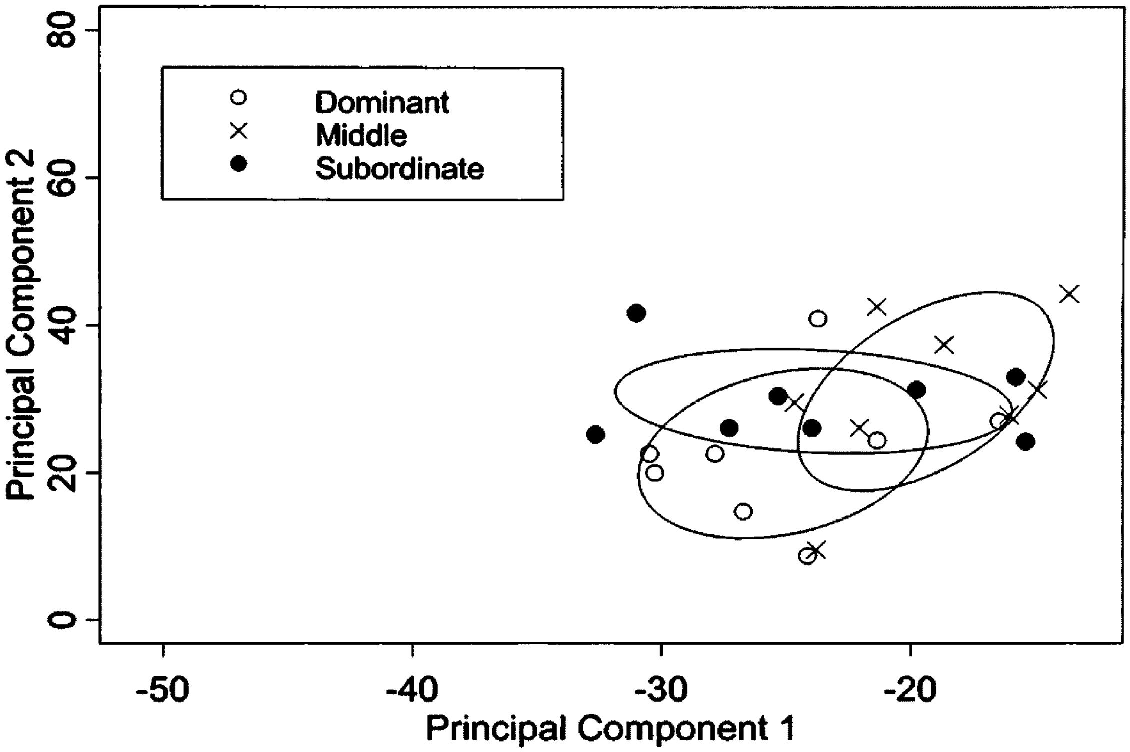

Figure 12. Principal components biplot for mixed-species flock treatment. Costs (i.e. vigilance and displacements) increase along the y-axis (PC2), and benefits (seed consumption, percentage eaten, and lower handling times) increase along the x-axis (PC1). Ellipses represent 95% confidence areas around the centroid of each rank.

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