

**THE EFFECT OF PATCH SIZE AND COMPETITOR NUMBER ON
AGGRESSION AMONG FORAGING HOUSE SPARROWS**

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ABSTRACT

Johnson, Cheryl Ann. The effect of patch size and competitor number on aggression among foraging house sparrows

To test between the contradictory predictions of resource defence theory and a modified hawk-dove model, I examined the effect of patch size and competitor number on aggression among foraging house sparrows, *Passer domesticus*. The birds were observed at feeding tables of seven different sizes, each table doubling in surface area from 0.014 m² to 0.922 m², allowing for a broader quantitative description of changes in aggression with patch size than previously examined. Resource defence theory predicts that small patches will be more defensible than large patches and that aggression will peak at intermediate competitor numbers at defensible patches. In contrast, a modified hawk-dove model predicts an increase in aggressiveness with competitor number; the model makes no predictions about patch size. Contrary to resource defence theory, birds did not defend an entire patch, even when it was as small as 0.014 m². As a result, aggression among the birds decreased more gradually with increasing patch size than expected by an all-or-none threshold model of resource defence. Moreover, birds fought more frequently and intensely at high competitor numbers, a result that is more consistent with the predictions of a modified hawk-dove model than the dome-shaped relationship predicted by models of resource defence. Interestingly, females were more aggressive and foraged faster than males. Because females were able to compete more effectively when individuals were aggressive, the proportion of females increased as patch size decreased. My results have implications for the truncated phenotype ideal free distributions.

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INTRODUCTION

The degree of food patchiness in the environment often influences aggressiveness in animal groups (Isbell 1991; Milinski & Parker 1991). In patchy environments, an animal that finds a small food patch may defend and monopolize the entire patch because small areas are less costly to defend than large areas (Schoener 1983). Conversely, when prey are dispersed over a large area, an individual may waste valuable time trying to exclude competitors from a large undefendable patch. Hence, resource defence theory (see Grant 1993) predicts a rapid decline in aggression above an upper threshold for patch size where defence is uneconomical. Empirical tests of resource defence theory show that many fish (e.g. Rubenstein 1981; Robb & Grant 1998), birds (e.g. Theimer 1987; Goldberg et al. 2001), and mammals (e.g. Monaghan & Metcalfe 1985; Isbell 1991) abandon defence when patches are large. However, because most studies only use two or three patch sizes (reviewed in Grant 1993; also see Grant & Guha 1993; Robb & Grant 1998), there has been no quantitative description of changes in defence behaviour over a wide range of patch sizes.

The number of competitors at a patch can also influence economic defendability. Resource defence theory predicts that when few competitors compete for patches, the low encounter rates among foragers and high relative food abundance (i.e. low competitor-to-resource ratio, Grant et al. 2000) will make defence unnecessary. Because relative food abundance decreases as competitor numbers increase (competitor-to-resource ratio, Grant

et al. 2000), an individual is predicted to become more aggressive with increasing competitor number in order to secure a larger proportion of the resources. However, when competitors numbers are extremely high, the high encounter rates among competitors and relative low food abundance (i.e. high competitor-to-resource ratio, Grant et al. 2000) may make aggression uneconomical. An individual may acquire more food through scramble competition than wasting valuable foraging time attempting to defend a patch against multiple intruders. Accordingly, resource defence theory predicts a dome-shaped relationship between aggression and competitor number with foragers defending and monopolizing patches at intermediate competitor numbers. Although several studies report that individuals abandon defence when competitors are abundant (Jones 1983; Marzluff & Heinrich 1991; Chapman & Kramer 1996), few studies show the predicted dome-shaped relationship between aggression and competitor number. Japanese medaka fish, *Oryzias latipes*, are most aggressive at intermediate competitor-to-resource ratios; however Grant et al. (2000) manipulated both competitor number and prey abundance in their study. The best evidence for the dome-shaped relationship between aggression and competitor number comes from Zenaida doves, *Zenaida aurita*, defending small, predictable patches of food (Goldberg et al. 2001).

When an entire patch cannot be defended, animals may share patches with others; rather than attempting to fight and chase all intruders from a patch, individuals may fight only with competitors feeding in the immediate vicinity. The aggression observed within a shared patch may be more appropriately described by a modified hawk-dove model

(Sirot 2000) than by a resource defence model. Sirot's (2000) model assumes that individuals fight for food items rather than an entire patch and that individuals interact with only one competitor at a time. Thus, unlike models of resource defence that assume defence against multiple intruders at high competitor number renders aggression uneconomical (i.e. high competitor-to-resource ratio, Grant et al. 2000), Sirot's (2000) model assumes that aggression remains effective at high competitor numbers because fights are always between two contestants (i.e. competitor-to-resource ratio = 2). Hence, contrary to the dome-shaped relationship predicted by resource defence, the modified hawk-dove model predicts that animals will become progressively more aggressive as competitor numbers increase due to an increase in the frequency of pairwise encounters. Several studies report such increases in aggression with competitor number when foragers share large patches (Monaghan & Metcalfe 1985; Prior & Weatherhead 1991; Goldberg et al. 2001; but see Elgar 1987). I know of no study, however, that documents aggressiveness over a wide range of competitor numbers (but see Syarifuddin & Kramer 1996).

Whether individuals share or defend a patch, ecological conditions promoting aggressiveness will likely result in the unequal sharing of resources among competitors, particularly if a dominance hierarchy exists. When animals defend patches, dominant individuals may obtain more food than subordinates by aggressively excluding subordinates from the patch (e.g. Marzluff & Heinrich 1991; Grant & Guha 1993; Chapman & Kramer 1996). Similarly, when animals share a patch, the increased intensity

and/or frequency of aggression from dominants may interfere with the foraging activities of subordinates causing their intake rates to decline with increasing competitor numbers. For example, an increased investment in the time spent monitoring potentially aggressive conspecifics causes the intake rates of subordinate house sparrows to decrease with increasing competitor number at a patch size of 0.36 m² (Johnson et al. 2001; also see Gray 1994). Aggression will most likely force subordinates to seek alternative food patches where aggression is less frequent and/or intense, whereas dominants will likely forage primarily in patches favouring the use of aggression (e.g. rich patches of food, Inman 1991; Gray 1994). As a result, a truncated phenotype distribution (Parker & Sutherland 1986; Tregenza 1995) may occur where the competitive abilities of individuals are correlated with patch quality.

The goal of the present study is to explore the effect of patch size and changes in competitor numbers on the rate and intensity of aggression among foraging house sparrows, *Passer domesticus*. I used seven patch sizes, the largest patch having a surface area 65 times greater than the smallest patch, allowing for a broader quantitative description of changes in aggressive behaviour than previously examined. House sparrows are an ideal test species because they compete aggressively for food and have a dominance hierarchy (Barnard 1981; Elgar 1987) with females being the more aggressive sex in the non-breeding season (see Summer-Smith 1988, but see Lowther & Cink 1992). Moreover, males have a black throat bib and can easily be distinguished from females (Summer-Smith 1988). Specifically, I expected small patches to be more defensible than

large ones and thus predicted 1) a rapid decline in aggression with increasing patch size, 2) a peak in aggression at intermediate competitor numbers and 3) a female biased sex ratio when patches are defensible.

METHODS

Study site and experimental design

The house sparrows were observed on 35 days between October 16 to December 17, 1998, in a residential backyard of Montréal, Canada (40°30' N, 73°40' W). The site was enclosed by fences. The feeding table (with a 1.5 cm plastic rim; see below) was elevated 25 cm from the ground and placed in the north-westerly corner of the site. The number of house sparrows visiting the site varied daily from 20 to 50 birds.

I manipulated patch size using square feeding tables of seven different sizes (0.014, 0.029, 0.058, 0.116, 0.230, 0.462, and 0.922 m²), each table doubling in surface area from the smallest to the largest patch; birds were presented with a single patch at a time. Seed density was kept constant among the patch size treatments at 870 ml/m² of white millet seed spread evenly over each patch surface, resulting in an increase in total amount of seed with patch size. I replenished the seed when about one third of its surface was bare (determined visually) and no birds were present at a patch. This method minimized depletion such that small patches (e.g. 0.029 m²) were replenished when about

67 percent of the initial seed weight remained at the patch (unpublished data, C.A. Johnson, L.-A. Giraldeau & J.W.A. Grant). All seven patch sizes were presented to the birds in random sequence before repeating the procedure five times per patch size treatment for a total of 35 trials (7 patch sizes X 5 replicates).

Because time of day affects aggression among foraging house sparrows (Barnard 1981), one trial was conducted per day (between 0700 and 1000 h). The ambient temperature (to the nearest 1 °C) was recorded at the onset of each trial to test for possible effects of temperature on the number of birds and rate of aggression at a patch (Caraco 1979; Barnard 1981). Because the birds were observed outside the breeding season (Summer-Smith 1988), aggression was not the result of competition for mates. A trial consisted of several short bouts when birds foraged interspersed with periods with no birds at the patch. On average, the number of birds at the patch changed every 3.0 ± 0.2 s ($\bar{x} \pm$ SE) during a foraging bout. The duration of the bouts was recorded using a stopwatch. A trial was ended when the cumulative foraging time reached 10 min or when birds were absent from the patch for more than 25 min ($\bar{x} \pm$ SE foraging time per trial = 9 min 56.5 s \pm 19.4s).

The trials were filmed from a tripod using a Super-VHS video-recorder with a timer. The following data were recorded from the video tapes: the number and duration of all aggressive encounters; the sex of the initiator and the recipient of aggression; and the times corresponding to changes in the number of birds at the patch. Aggressive

encounters included wing flapping, lunging and biting (see Table 1; Summers-Smith 1988; Lowther & Cink 1992) and ended when foraging resumed. The number of females and males at a patch were counted during scan samples taken every 15 s for each trial. During a trial, a male and female bird were haphazardly chosen from those foraging at a patch every 2 min and observed until the bird left the patch. The number of seeds eaten and the changes in the number of birds at a patch were recorded for each focal bird.

Data Analysis

Because I could not identify individual birds, I used the mean of the observations per trial as a datum in my analyses to meet the statistical assumption of independence (Lima 1995). I weighted the number of birds observed at a patch during a trial by the cumulative time spent foraging at that number (minimum 3 s) before calculating the mean weighted number of birds per trial. I also recorded the maximum number of birds at a patch per trial. Rate of aggression was quantified as the total rate of aggression (total interactions/min). To control for the opportunity for aggression (i.e. number of individuals actually competing at a patch), I also calculated the per capita rate of aggression (interaction/min/bird; see Robb & Grant 1998) for each number of birds observed at a patch, weighted by time (see above). I omitted data for solitary birds when calculating the weighted mean per capita rate of aggression per trial to avoid underestimating aggression. Following Lowther and Cink (1992), aggressive encounters were scored according to intensity; escalated fights, defined as fights most costly in terms of energy expenditure

and risk of injury (Archer 1988), received a score of 5 (Table 1). My measure of aggressive intensity, referring only to instances when birds fought, was the mean aggressive score per trial.

To estimate sex ratio for each trial, I calculated the mean proportion of females at a patch from the total males and females counted during scan sample taken every 15 s. To determine whether aggressiveness differed between the sexes, I calculated the weighted mean per capita rate and intensity of aggression initiated by females and males. I also calculated the weighted mean per capita rates of aggression received by each sex. Two-way ANOVAs were used to determine whether aggression differed between the sexes among the patch size treatments.

I measured intake rate as the number of seeds eaten per unit time a focal bird was observed foraging at a patch. To control for the possible effects of changes in competitor numbers on intake rates, I calculated the mean number of birds at a patch for each bird observed. Three to five foraging females and males ($N = 6-10$ birds in total) were each observed from 5 to 42 s ($\bar{x} = 18$ s) per trial. I pooled the intake rate data per trial by sex and used the overall mean intake rate per patch size as a datum in my analysis.

Differences in intake rates between the sexes among the patch size treatments were tested using an ANCOVA, with bird density as a covariate.

I \log_{10} transformed patch area for all analyses because it was a geometric series.

Neither the aggressive intensity data, nor the intake rate data required transformation. However, the proportion of females were arcsine-square-root-transformed, and the remaining dependent variables were \log_{10} transformed to satisfy the assumption of normality for parametric tests. Values reported in the text have been backtransformed. I report second order polynomial regressions only when the partial-t value for the quadratic term was significant after entering the linear term into the model. For all ANCOVA models, I only mention interactions with covariates when statistically significant ($P \leq 0.05$); non-significant interactions were removed from the models (Freud & Littell 1981). Temperature (range: -10 to 3°C) was omitted from the analyses because it had no detectable effect on the number of birds at a patch, the rate of total aggression, or per capita aggression (ANCOVA: $P_s \geq 0.24$) in my study. Also, no temporal trends in the number of birds, or total or per capita rate of aggression were detected during 30-s intervals of each trial (MANOVA: $P_s \geq 0.40$).

RESULTS

General Results

House sparrows normally arrived to feed 5-10 min after the seeds were placed at the patch. Most birds fed at the patch when presented with the larger patch sizes. However, an increasing number of birds fed on the ground near the patch when presented with the

smaller patch sizes.

Birds landed on the fence prior to feeding and returned to it when fleeing from an aggressor (i.e intensity score = 5). Although more birds were observed fleeing from small versus large patches (frequency $\bar{x} \pm SE$ at the 0.014 versus the 0.922 m², respectively: 4.1 \pm 0.96 versus 0.40 \pm 0.22), aggression was not used to exclude others from small patches. Rather than defend the entire patch, birds attacked individuals feeding in the immediate vicinity, perhaps using aggression to maintain individual distances (see Lowther & Cink 1992). Fights never involved more than two birds at a time.

The Effect of Patch Size

Fewer house sparrows foraged at small patches than large patches. The maximum number of birds increased from 4.7 birds at the smallest patch to 23 birds at the largest patch (Quadratic regression: $R^2 = 0.90$, $F_{2,32} = 144.96$, $P < 0.00004$; partial t: $t = -2.07$, $P = 0.047$; Fig. 1a). In comparison, the mean number of birds increased from 2.5 at the smallest to 7.5 birds at the largest patch (Linear regression: $R^2 = 0.74$, $F_{1,33} = 92.37$, $P \ll 0.00001$; Fig. 1a), corresponding to about one-half and one-third of the maximum number of birds at the respective patch sizes. In contrast, the maximum (Quadratic regression: $R^2 = 0.96$, $F_{2,32} = 396.11$, $P \ll 0.0001$; partial t: $t = -5.09$, $P \ll 0.0001$) and mean (Quadratic regression: $R^2 = 0.95$, $F_{2,32} = 335.17$, $P \ll 0.00001$; partial t: $t = -4.06$, $P = 0.0003$) bird density decreased with increasing patch size (Fig. 1b). Thus, despite the presence of fewer

birds, individuals foraged closer to each other at small patches. The maximum bird density decreased 14 fold from 338.8 at the smallest to 24.3 birds/m² at the largest patch, whereas the mean bird density decreased 21 fold from 175.8 to 8.2 birds/m². Maximum bird density was nearly twice the mean at the smallest patch but 3 times larger than the mean at the largest.

House sparrows were less frequently aggressive with increasing patch size. The total rate of aggression remained relatively constant at 4 interactions/min for the three smallest patches, but decreased to 0.7 interactions/min at the largest patch (Quadratic regression model: $R^2 = 0.41$, $F_{2,32} = 11.33$, $P = 0.0002$; partial t: $t = -2.02$, $P = 0.035$; Fig. 2a). In contrast to the rapid decrease predicted with resource defence, per capita rate of aggression decreased continuously with increasing patch size (Quadratic regression: $R^2 = 0.75$, $F_{2,32} = 46.71$, $P \ll 0.0001$; partial t: $t = -2.22$, $P = 0.034$; Fig. 2b) from 1.5 at the smallest to 0.07 interactions/min/bird at the largest patch, respectively.

Overall, 69 % (774/1115) of all observed aggression involved physical contact between birds with 76% (586/774) of these interactions receiving a score of 3 (see Table 1). In contrast to the frequency of aggression, the intensity of aggression did not decrease significantly with increasing patch size (Spearman rank correlation: $r_s = -0.27$, $N = 35$, $P = 0.11$). Escalated fighting (i.e score = 5) represented only 6% of all interactions. The percentage of escalated fights did not decrease significantly with increasing patch size (Spearman rank correlation: $r_s = -0.33$, $N = 35$, $P = 0.062$).

The Effect of Group Size and Bird Density

To examine the effect of the number of birds at a patch (group size) on aggression, I calculated the mean per capita rates and intensity of aggression ($N = 5$ replicates) for each observed group size of 2 or more birds for the seven patch size treatments. To avoid zero values (see Stewart-Oaten 1996), I removed data from the analyses when the cumulative time a given number of birds spent at each patch ($N = 5$ replicates combined) was less than 30 s. The few remaining zero values for per capita rates of aggression were averaged with the non-zero value for the next largest group size. For example, a per capita aggression rate of zero for 3 birds and 2 for 4 birds averaged to 1 interaction/min/bird for 3.5 birds at a particular patch. I tested for trends in the rate and intensity of aggression versus number of birds among the patch size treatments using an ANCOVA with group size as a covariate.

The effect of the number of birds on the per capita rate of aggression differed among the patch size treatments (Fig. 3a), as indicated by a significant interaction between patch size and number of birds ($F_{6,65} = 4.38, P = 0.001$). Hence, I used regression models to determine the effect of number of foragers on per capita rate of aggression for each patch size separately. Although there was no detectable effect of the number of birds on the per capita rate of aggression at the smallest patch ($P = 0.07$), per capita rate of aggression increased significantly with the number of birds foraging for patch sizes 0.029 through 0.230 m² (Regression model: $P_s \leq 0.016$; Fig. 3a). In fact, per capita rate of

aggression increased at an accelerating rate at the 0.029 m² patch (partial t: $t = 3.75$, $P = 0.033$), but at a decelerating rate at the 0.230 m² patch (partial t: $t = -2.80$, $P = 0.015$; Fig. 3a). Number of birds had no effect on aggression at the two largest patches ($P_s \geq 0.23$). In general, the strength of the relationship between per capita rate of aggression and number of birds decreased with increasing patch size (Fig. 3a).

To examine whether crowding was responsible for the high per capita rate of aggression at the small patches, I used an ANCOVA with \log_{10} bird density as the covariate. Per capita rate of aggression was still higher at small compared to large patches after controlling for changes in bird density ($F_{6,71} = 6.97$, $P \ll 0.0001$; Fig. 3b). Contrary to the dome-shaped relationship predicted by resource defence theory, per capita rate of aggression increased with bird density after controlling for differences in patch size ($F_{1,71} = 49.93$, $P \ll 0.000001$; Fig 3b).

House sparrows also fought more intensely as the number of foragers increased at a patch (ANCOVA: $F_{6,71} = 2.95$, $P = 0.013$) and as the size of a patch decreased ($F_{1,71} = 9.38$, $P = 0.003$; Linear polynomial contrast: $\beta \pm SE = -0.921 \pm 0.264$, $P = 0.001$; Fig. 4a). Because the relationship between intensity of aggression and bird density was non-linear (Quadratic regression: $F_{2,76} = 9.90$, $P = 0.002$; partial t: $t = -2.04$, $P = 0.044$), I used residuals from a regression of intensity of aggression versus bird density to test whether the aforementioned effect of patch size was a result of higher bird densities. The analysis revealed that the increase in intensity of aggression was primarily caused by crowding at

the smaller patches; there was no effect of patch size after controlling for differences in bird density (Linear regression: $F_{1,77} = 0.52$, $P = 0.59$), whereas aggression increased with competitor density after controlling for patch size (Quadratic regression: $F_{2,76} = 5.16$, $P = 0.008$; partial-t: $t = -2.39$, $P = 0.022$; Fig. 4b).

The Effect of Sex

Both males and females became less aggressive as patch size increased (Two-way ANOVA: $F_{6,56} = 17.19$, $P \ll 0.00001$; Fig. 5a). Females were more aggressive than males, judging from the rate they initiated attacks ($F_{1,56} = 34.68$, $P < 0.00001$; Fig. 5a); there was no patch size by sex interaction ($F_{6,56} = 1.03$, $P = 0.41$). Most of the aggression initiated by females was directed towards females, making up 49% (545/1115) of all aggression compared to 29% (322/1115) for female-male interactions. Males were also more aggressive towards females, attacking them 1.4 times more often than other males (13.1 versus 9.1% of all aggression, respectively). Despite the tendency for both sexes to attack females, the per capita rate of aggression received did not differ between females and males ($F_{1,56} = 1.55$, $P = 0.22$); both sexes received aggression less frequently as patch size increased ($F_{6,56} = 21.09$, $P \ll 0.0001$; Fig. 5b). Fights were also more intense when initiated by females than males ($F_{1,56} = 4.52$, $P = 0.038$); there was no overall effect of patch size ($F_{6,56} = 1.44$, $P = 0.22$), nor a significant patch size by sex interaction ($F_{6,56} = 0.84$, $P = 0.55$).

The proportion of females decreased slightly with increasing patch size (Linear regression: $R^2 = 0.14$, $F_{1,33} = 5.39$, $P = 0.027$; Fig. 6). I examined the effect of bird density on the proportion of females among the patch size treatments. A significant patch size by density interaction (ANCOVA: $F_{6,71} = 3.00$, $P = 0.011$) indicated that the effect of bird density on the proportion of females varied among patch size treatments. Hence, I used regression models to determine the effect for each patch size treatment. The proportion of females increased with bird density for all but two patch sizes (see Table 2). However, only birds competing at the 0.058 m^2 experienced a significant increase in the proportion of females with bird density.

Intake Rate

The birds fed faster as the density of competitors increased (ANCOVA: $F_{1,55} = 6.17$, $P = 0.016$), but there was no overall effect of patch size on intake rates ($F_{6,55} = 1.19$, $P = 0.12$; Fig. 7). Females fed faster than males, consuming on average 1.3 seeds/s compared to 1.1 seeds/s for males (ANCOVA: $F_{1,55} = 12.03$, $P = 0.001$); there was no significant patch size by sex interaction ($F_{6,55} = 0.39$, $P = 0.89$).

DISCUSSION

My results suggest that both patch size and competitor number influence aggressiveness

among animals in groups. Contrary to my expectations, the house sparrows did not attempt to defend the entire patch, not even when it was as small as 0.014 m². As a result, the observed decrease in aggression with increasing patch size was more gradual than the rapid decline expected if there had been an upper threshold of patch size for defence. Moreover, contrary to the dome-shaped relationship between aggression and competitor number predicted by resource defence theory, aggressiveness among the house sparrows increased with competitor number with no sign of a decrease. The increased frequency and intensity of aggression at high competitor numbers is consistent with the prediction of Sirot's (2000) model, suggesting that the modified hawk-dove model may provide a better description of aggressive behaviour among the birds in my study than models of resource defence.

Per capita rate of aggression among the house sparrows decreased 21 fold from the smallest to the largest patch. With the exception of a 37 fold decrease observed in Monaghan & Metcalfe's (1985) study, the magnitude of the change reported in my study is greater than the 1.1 to 10.5 fold decrease in per capita rates of aggression observed in previous studies (calculated from Rubenstein 1981; Theimer 1987; Grant & Guha 1993; Robb & Grant 1998; Goldberg et al. 2001). However, by extending my examination over a large range of patch sizes, I showed that aggression decreased continuously with increasing patch size. Grant (1993) suggests that individual differences in thresholds of behavioural responses may make the transition from the defence of small patches to the non-defence of larger patches more continuous than an all-or-none threshold model.

However, this explanation seems unlikely given that the birds used aggression only when competitors came too close. This behaviour is consistent with the assumptions of the modified hawk-dove model where individuals only attack competitors feeding in the immediate vicinity (see Sirot 2000). Although previous hawk-dove models have examined the effect of hunger (Houston & McNamara 1988), food abundance and competitor density (Sirot 2000) on aggressiveness in animals groups, my study is the first to implicate patch size as an ecological variable influencing aggression when individuals share patches.

In my study, contests never involved more than two birds; due to an increase frequency of pairwise encounters, aggression increased with increasing competitor number for all patch sizes. Interestingly, the strength of the relationship between aggression and competitor number increased with decreasing patch size. Consequently, aggression increased progressively with competitor density as predicted by Sirot's (2000) modified hawk-dove model. Elgar (1987) showed a similar result but only for two patch sizes of 0.023 m² and 1 m². The observed increase in aggression may have been due to the even distribution of seeds decreasing the probability that individuals would encounter multiple competitors at a time; the increased effectiveness of aggression when it involves only two individuals (i.e. competitor-to-resource ratio = 2, Grant et al. 2000) presumably resulted in birds securing a larger proportion of seeds by displacing conspecifics than scrambling for food. Carrion feeding birds are also more aggressive at high competitor numbers when feeding on several small carcasses dispersed over a patch (Prior &

Weatherhead 1991). However, when carrion feeding birds forage at a single large carcass, they become less aggressive at high competitor numbers (Marzluff & Heinrich 1991), perhaps because discrete, localized clumps of food promote fights between three or more contestants rendering aggression ineffective at high competitor numbers as assumed by resource defence theory (i.e. high competitor-to-resource ratio, Grant et al. 2000). Hence, models of resource defence may accurately describe aggression among some fish (Grant & Guha 1993; Jones 1983), frugivorous primates (see Isbell 1991), and other animals feeding on discrete, localized clumps of prey. Conversely, the modified hawk-dove model may better describe aggression among foragers whose prey is more dispersed and may promote contests between only two individuals, such as oystercatchers feeding on mussels (Sirot 2000) and folivorous primates (see Isbell 1991).

Females initiated attacks more frequently and fought more intensely than males, allowing them to compete more effectively particularly at small patch sizes. The proportion of females increased at small patches and tended to increase with competitor number. As with starlings, *Sturnus vulgaris* (Inman 1990; also see Gray 1994), males most likely avoided feeding near dominant females, perhaps preferring to feed on the ground rather than at the patch so as not to experience rapid declines in intake rates due to aggression (see Gray 1994; Johnson et al. 2001). Dominant individuals tend to be less susceptible to the interference caused by increased aggression (Gray 1994; Johnson et al. 2001). Hence, the increase in proportion of females at patches when individuals aggressively competed for food may explain why intake rates remained unchanged among

the patch size treatments and increased slightly with bird density. In contrast to my results, Elgar (1987) found that increased aggression among house sparrows at small patches resulted in lower intake rates compared to large patches. However, his birds were primarily males (Elgar 1987) and may have been more vulnerable to aggression.

In summary, the changes in aggressive behaviour among the birds in my study were more consistent with the sharing of food patches than with resource defence; the birds were most aggressive not only at small patches but at high competitor densities. The impact of reducing patch size on animal distributions and mortality rates are likely different for populations sharing resource patches than those defending them. When crowding at small patches causes fighting to become uneconomical, low rates of aggression may allow poor competitors to invade patches, particularly if the patch is rich in food. For example, a decrease in aggression among dominant fish at high competitor density allows subordinates to invade patches and obtain more food items than when competitor numbers are low and dominants monopolize the patch (Tregenza et al. 1996). In contrast, when crowding at small patches results in increased aggression, the high rates and intensity of aggression may lead to a truncated phenotype distribution whereby poor competitors are forced to occupy poorer quality patches (Parker & Sutherland 1986; Sutherland 1992; Sutherland & Parker 1992). For example, young oystercatchers supplement their intake rates more than older birds in poor quality habitats where the risk of predation is high (Caldow et al. 1999; also see Goss-Custard & Durell 1988), perhaps because they avoid areas where high competitor densities result in high aggression (Ens &

Goss-Custard 1984). Future studies should investigate the effect of patch size and concomitant changes in competitor density on habitat choice and its consequences to survival, particularly for species that become more aggressive under crowded conditions.

Figure 1. Changes in ($\bar{x} \pm SE$, $N = 5$) a) mean number (■, $\log_{10}(\text{number}) = 0.963 + 0.271\log_{10}(x)$) and maximum number (○, $\log_{10}(\text{max. number}) = 1.403 + 0.223\log_{10}(x) - 0.078\log_{10}(x^2)$); and b) mean density (■, $\log_{10}(\text{bird density}) = 0.884 - 1.044\log_{10}(x) - 0.180\log_{10}(x^2)$) and maximum density (○, $\log_{10}(\text{max. density}) = 1.375 - 0.925\log_{10}(x) - 0.175\log_{10}(x^2)$) of foraging house sparrows in relation to patch size. Note the logarithmic scale for both axes.

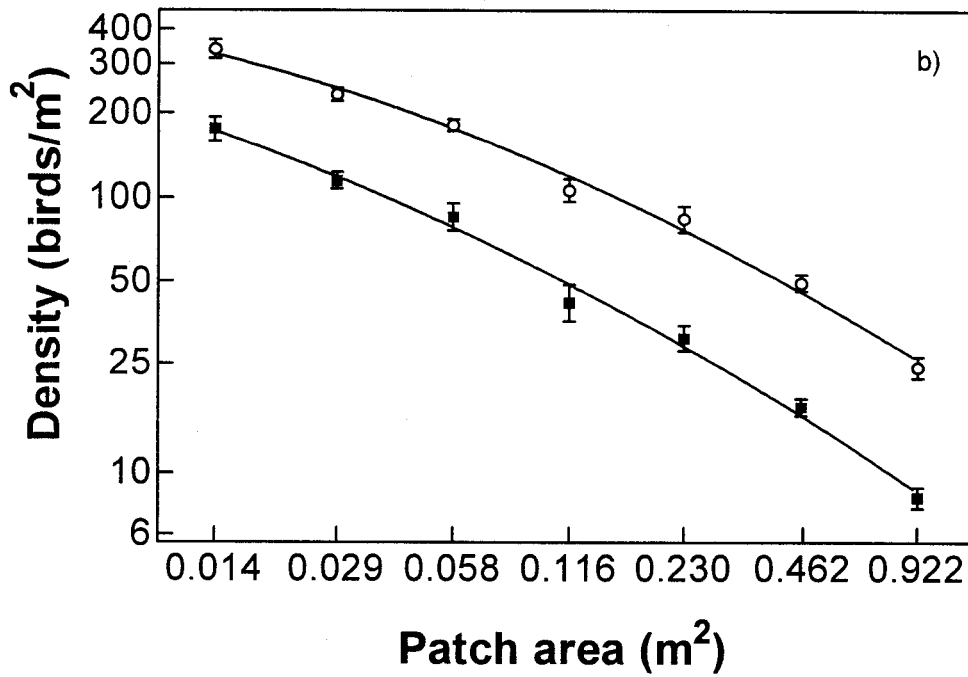
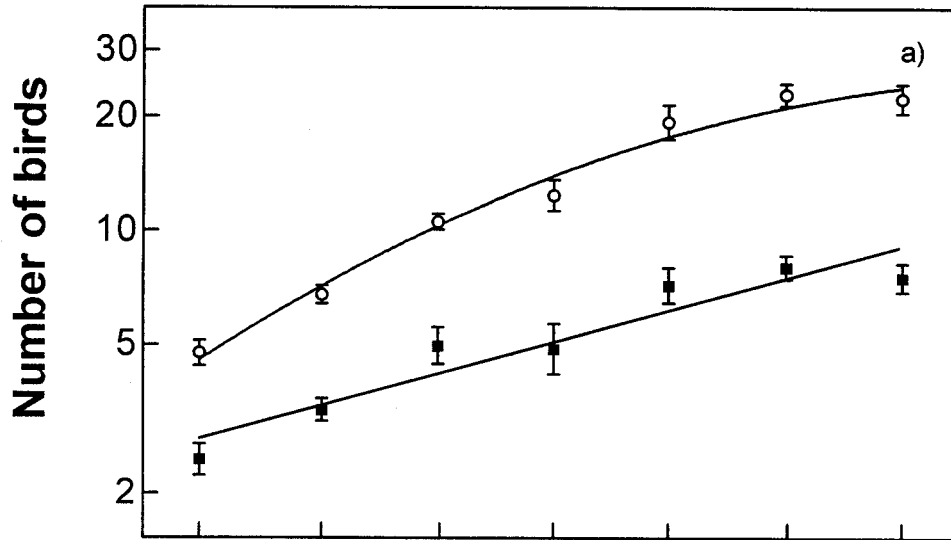


Figure 2 The mean ($\bar{x} \pm SE$, $N = 5$) rate of a) total aggression ($\log_{10}(\text{total aggression}) = -0.121 - 0.935\log_{10}(x) - 0.295\log_{10}(x^2)$) and b) per capita aggression ($\log_{10}(\text{per capita aggression}) = -1.162 - 1.189\log_{10}(x) - 0.261\log_{10}(x^2)$) among the foraging birds in relation to patch size. Note the logarithmic scale for both axes.

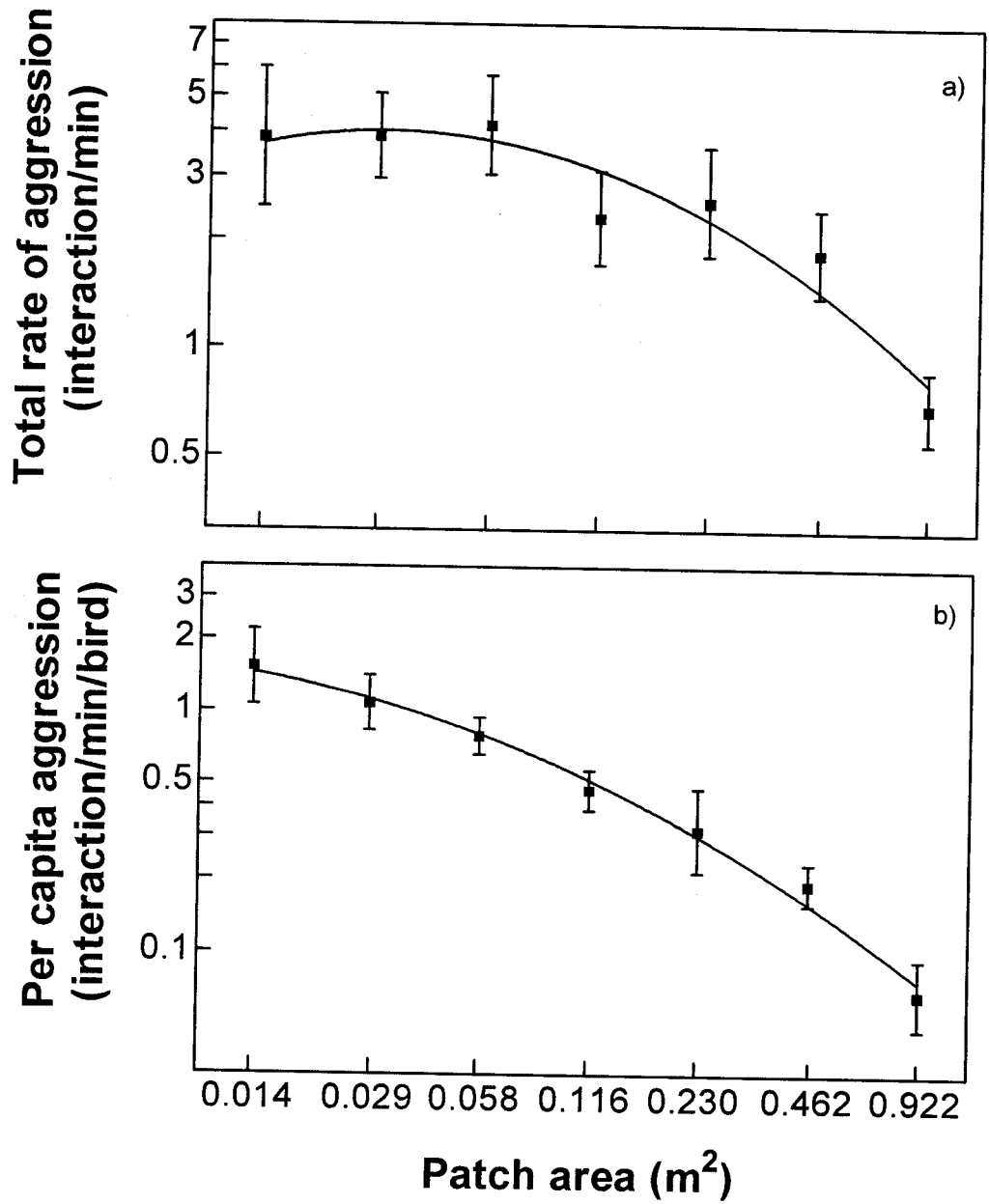


Figure 3 The per capita rate of aggression (\bar{x} of 5 replicates) versus a) number of birds; and b) bird density for all patch size treatments (■ = 0.014 m²; ▲ = 0.029 m²; ● = 0.058 m²; ▼ = 0.116 m²; ○ = 0.230 m²; □ = 0.462 m²; △ = 0.922 m²). Dashed lines denote non-significant regressions. Note the scaling of the axes.

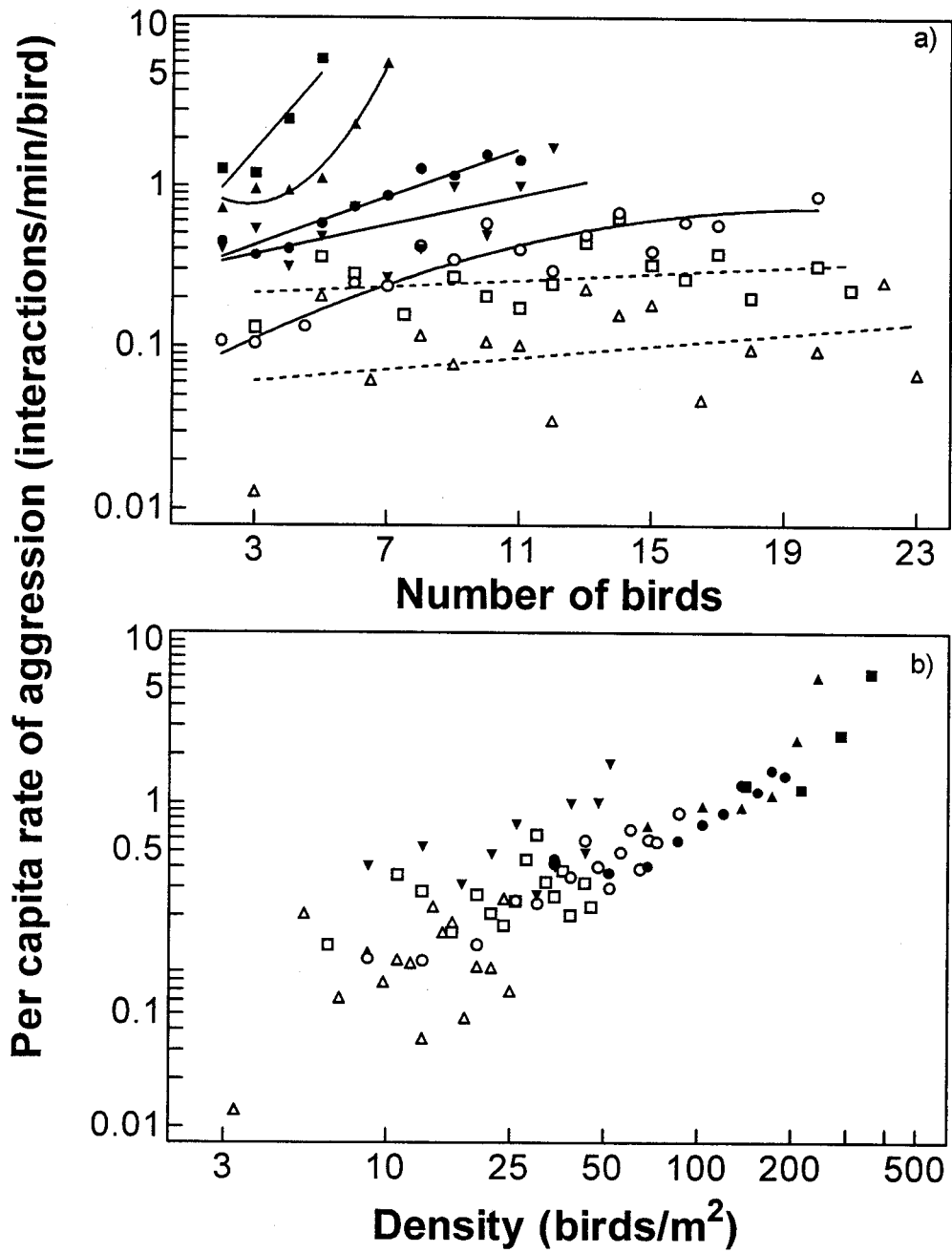


Figure 4 The intensity of aggression (\bar{x} of 5 replicates) versus a) number of birds; and b) bird density for all patch size treatments (■ = 0.014 m²; ▲ = 0.029 m²; ● = 0.058 m²; ▼ = 0.116 m²; ○ = 0.230 m²; □ = 0.462 m²; △ = 0.922 m²). Note the logarithmic scaling of the x-axis in b).

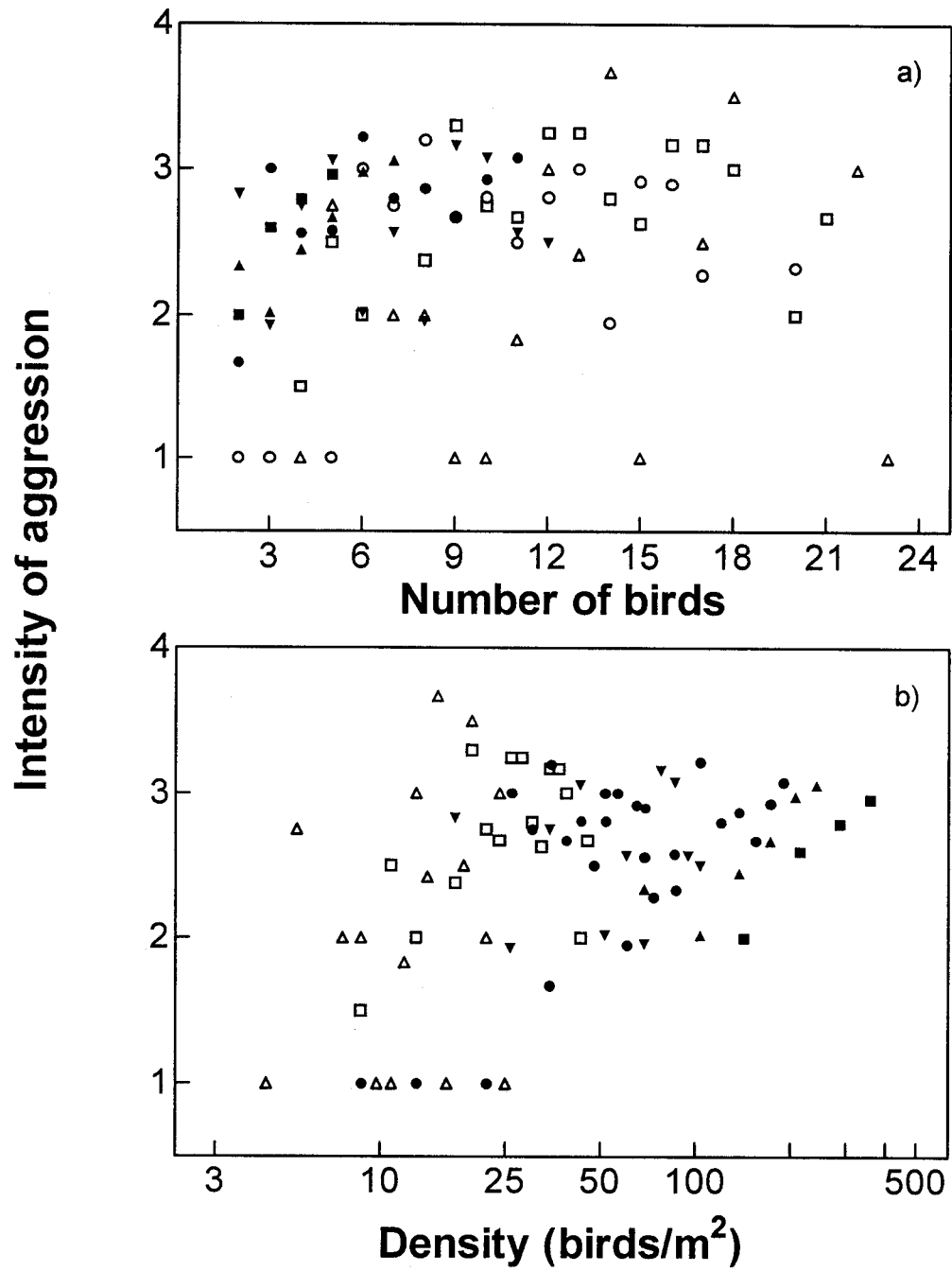


Figure 5 a) Mean ($\bar{x} \pm SE$, $N = 5$) per capita rate of aggression a) initiated ($\log_{10}(y + 0.1)$) and b) received by females (■) and males (□) versus patch size. Note the logarithmic scaling of the x-axes.

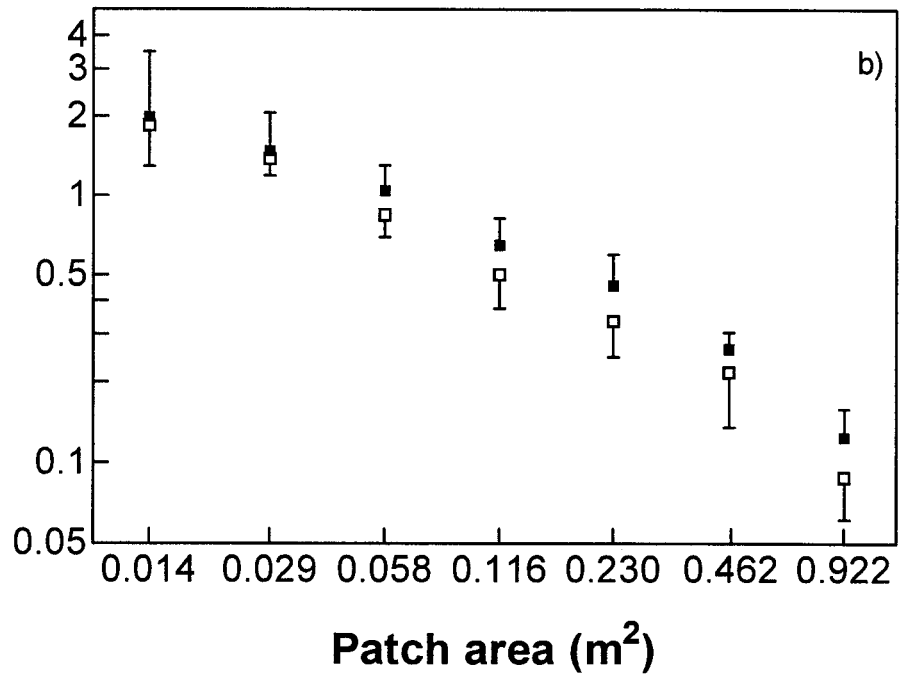
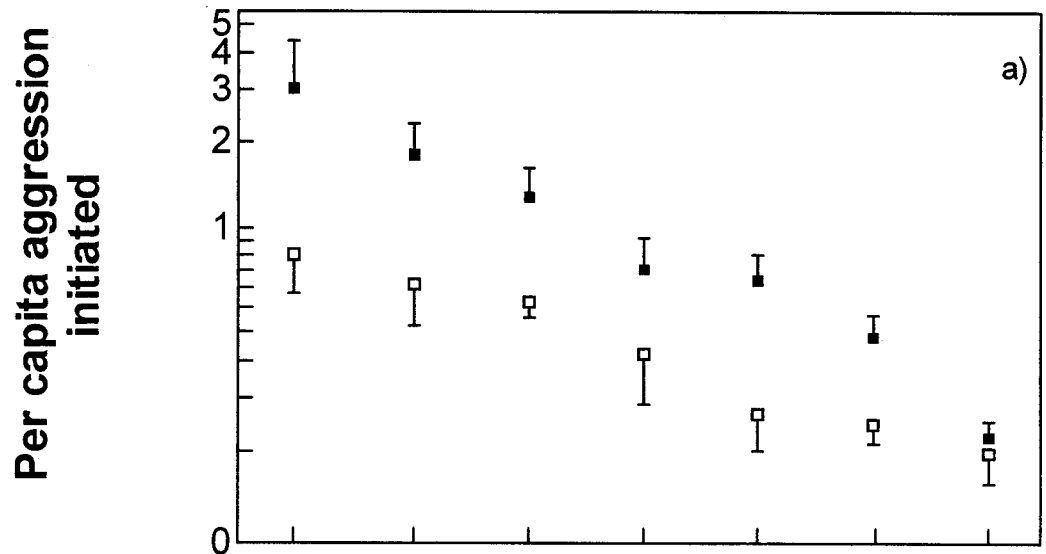


Figure 6 The proportion of females versus ($\bar{x} \pm SE, N = 5$) patch size. Note the logarithmic scale for x-axis and the arcsin-square root scale for the y-axis.

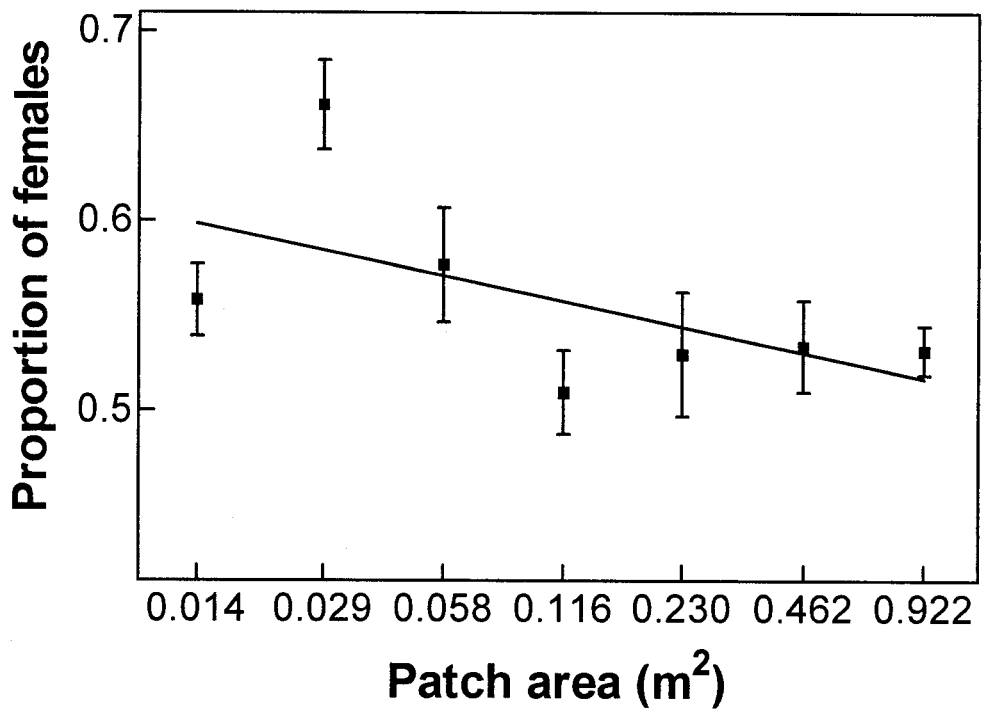


Figure 7 Mean ($\bar{x} \pm SE$, $N = 5$) intake rate for females (■) and males (□) among the patch size treatments. Note the logarithmic scaling of the x-axes.

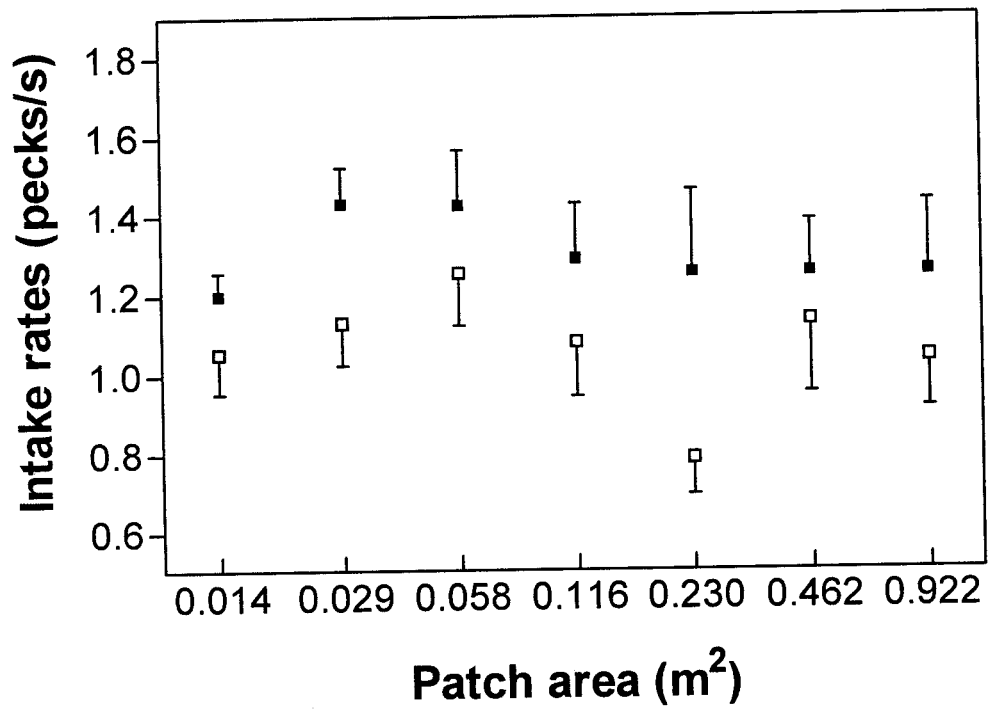


Table 1. Ranks characterizing the intensity of aggression according to observed behavioural patterns and duration (after Lowther & Cink 1992)

Score	Behaviour	Duration (s)
1	Wing flapping without physical contact.	~0.1-1.8
2	Lunging or hopping towards opponent with beak open; no physical contact.	~0.6-2.7
3	Physical contact: aggressor pecks (i.e touches with its beak) recipient 1 to 3 times, often displacing the recipient (i.e. remains on patch).	~0.2-2.3
4	Aggressor lands on recipient regardless if recipient is the only bird at the patch, pushes recipient with its legs and pecks it 1-3 times. Recipient leaves the patch.	~0.2-1.5
5	Aggressor pecks opponent and opponent retaliates resulting in 4-8 back-and-forth pecks with wing flapping. During the escalated fight, the birds stand in an upright position and erect their chest feathers. Loser leaves the patch.	~1.0-3.2

Table 2. The proportion of females versus bird density for each of the seven different path size treatments.

Patch size (m ²)	Slope ($\beta \pm \text{SE}$)	<i>P</i> -value
0.014	+0.340 \pm 0.129	0.119
0.029	-0.235 \pm 0.145	0.065
0.058	+0.161 \pm 0.065	0.038
0.116	+0.058 \pm 0.058	0.348
0.230	-0.040 \pm 0.038	0.311
0.462	+0.065 \pm 0.044	0.161
0.922	+0.048 \pm 0.048	0.335

REFERENCES

- Archer, J (1988) *The behavioral biology of aggression*. Cambridge: Cambridge University Press.
- Barnard, CJ (1981) Factors affecting flock size mean and variance in a winter population of house sparrows (*Passer domesticus* L.). *Behaviour* 74:114-127.
- Caldow, RWG, Goss-Custard, JD, Stillman, RA, Durell, SEA le V dit, Swifen, R & Bregnballe, T (1999) Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *J Anim Ecol* 68:869-878.
- Caraco, T (1979) Time budgeting and group size: a test of theory. *Ecology* 60:618-627.
- Chapman, MR & Kramer, DL (1996) Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Anim Behav* 52:83-94.
- Elgar, MA (1987) Food intake rate and resource availability: flocking decisions in house sparrows. *Anim Behav* 35:1168-1176.

- Ens, BJ & Goss-Custard, J D (1984) Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe Estuary. *J Anim Ecol* 53:217-231.
- Freud, RJ & Littell, RC (1981) *SAS for Linear Models*. Calgary: SAS Institute inc.; 187-205.
- Goldberg, JL, Grant, JWA & Lefebvre, L (2001) Effects of temporal predictability and the spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behav Ecol* 12:490-495.
- Goss-Custard, JD & Durell, SEA le V dit (1988) The effect of dominance and feeding method on the intake rates of oystercatchers, *Haematopus ostralegus*, feeding on mussels. *J Anim Ecol* 57:827-844.
- Grant, JWA (1993) Whether or not to defend? The influence of resource distribution. *Mar Behav Physiol* 23:137-153.
- & Guha, RT (1993) Spatial clumping of food increases its monopolization and defense by convict cichlids, *Cichlasoma nigrofasciatum*. *Behav Ecol* 4:293-296.
- Gaboury, CL, & Levitt, HL (2000) Competitor-to-resource ratio, a general

- formulation of operational sex ratio, as a predictor of competitive aggression in Japanese medaka (Pisces: Oryziidae). *Behav Ecol* 11:670-675.
- Gray, RD (1994) Sparrows, matching and the ideal free distribution: can biological and psychological approaches be synthesized? *Anim Behav* 48:411-423.
- Houston, AI & McNamara, JM (1998) Fighting for food: a dynamic version of the hawk-dove game. *Evol Ecol* 2:51-64.
- Isbell, LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2:143-155.
- Inman, AJ (1990) Group foraging in starlings: distributions of unequal competitors. *Anim Behav* 40:801-810.
- Johnson, CA, Giraldeau, L-A & Grant, JWA (2001) The effect of handling time on interference among house sparrows foraging at different seed densities. *Behaviour* 138: 597-614.
- Jones, GP (1983) Relationship between density and behavior in juvenile *Pseudolabrus celidotus* (Pisces: Labridae). *Anim Behav* 31:729-735.

Lima, SL (1995) Back to the basics of anti-predatory vigilance: the group-size effect.

Anim Behav 49:11-20.

Lowther, PE & Cink, CL, 1992. House sparrow. In: *Birds of North America*. Washington

D.C.: American Ornithologists' Union and Academy of Natural Sciences of

Philadelphia; 7-9.

Marzuluff, JM & Heinrich, B (1991) Foraging by common ravens in the presence and

absence of territory holders: an experimental analysis of social foraging. *Anim*

Behav 42:755-770.

Milinski, M & Parker, GA (1991) Competition for resources. In: *Behavioral Ecology: an*

Evolutionary Approach, 3rd ed (JR Krebs and NB Davies, eds). Oxford:

Blackwell Scientific Publications; 137-168.

Monaghan, P & Metcalfe, NB (1985) Group foraging in wild brown hares: effects of

resource distribution and social status. *Anim Behav* 33:993-999.

Parker, GA & Sutherland, WJ (1986) Ideal free distributions when competitors differ in

competitive ability: phenotype-limited ideal models. *Anim Behav* 34:1222-1242.

Prior, KA & Weatherhead, PJ (1991) Competition at the carcass: opportunities for social

- foraging by turkey vultures in southern Ontario. *Can J Zool* 69:1550-1556.
- Rubenstein, DI (1981) Population density, resource patterning, and territoriality in the everglades pygmy sunfish. *Anim Behav* 29:155-172.
- Robb, SE & Grant, JWA, 1998. Interactions between the spatial and temporal clumping of food affect the intensity of aggression in Japanese medaka. *Anim Behav* 56:29-34.
- Schoener, TW (1983) Simple models of optimal feeding-territory size: a reconciliation. *Am Nat* 121:608-629.
- Siro, E (2000) An evolutionary stable strategy for aggressiveness in feeding groups. *Behav Ecol* 11:351-356.
- Stewart-Oaten, A (1996) Sequential estimation of log (abundance). *Biometrics* 52:38-49.
- Summer-Smith, JD (1988) *The sparrows*. Calton: T and AD Poyser Ltd.
- Sutherland, WJ (1992) Game theory models of functional and aggregative responses. *Oecologia* 90:150-152.

--- & Parker, GA (1992) The relationship between continuous-input and interference models of ideal free distribution of unequal competitors. *Anim Behav* 44:345-355.

Syarifuddin, S & Kramer, DL (1996) The effect of space use and aggression at a concentrated food source in blue gouramis, *Trichogaster trichopterus*, (Pisces: Belontiidae). *Env Biol Fish* 46: 289-296.

Theimer, TC (1987) The effect of seed dispersion on the foraging success of dominant and subordinate dark-eyed juncos, *Junco hyemalis*. *Anim Behav* 35:1882-1890.

Tregenza, T (1995) Common misconceptions in applying the ideal distribution theory. *Anim Behav* 47:485-487.

---, Hack, MA & Thompson, DJ (1996) Relative competitive success of unequal competitors changes with overall density. *Oikos* 77:158-162.