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PHOENIX BOUCHARD-KERR

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To my parents,
who have always supported me
with love and encouragement.

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RÉSUMÉ

Lorsque les animaux s'approvisionnent en groupe, ils mangent souvent de la nourriture découverte par leurs congénères. Si la parcelle est divisible, les individus peuvent exploiter par cleptoparasitisme la nourriture découverte par d'autres, soit de manière passive ou de manière agressive. Dans un tel contexte, l'agressivité individuelle (c.-à-d. la probabilité d'être agressif lors d'une rencontre avec un compétiteur) est censée être influencée par plusieurs facteurs écologiques, explorés par des modèles économiques de défense des ressources. Par exemple, le niveau de connaissance que les animaux ont de la localisation des parcelles de nourriture est censé influencer l'agressivité ; cependant, peu d'études empiriques se sont penchées sur le sujet. Ce niveau de connaissance devrait influencer 1) le niveau d'agressivité individuelle et 2) l'effet que la densité des parcelles exerce sur le niveau d'agressivité. 1) Un modèle d'optimalité de défense des ressources prédit que l'agressivité devrait être plus élevée lorsque les individus connaissent la localisation des parcelles, parce qu'ils peuvent limiter leur recherche à une aire plus restreinte et donc plus défendable. 2) Des modèles de la théorie des jeux prédisent une diminution de l'agressivité lorsque la densité des parcelles augmente, parce que les parcelles de remplacement deviennent moins coûteuses à trouver. Cependant, lorsque la localisation des parcelles est inconnue, l'agressivité devrait rester inchangée à cause de l'incertitude quant à la disponibilité des parcelles de remplacement. Afin de tester ces prédictions expérimentalement, nous avons observé le comportement agressif de groupes de moineaux domestiques (*Passer domesticus*) en manipulant simultanément la densité des parcelles ainsi que la signalisation de la localisation de celles-ci. Les changements observés au niveau du taux d'agression semblent appuyer nos deux prédictions : 1) Le taux d'agression était plus élevé lorsque les parcelles étaient signalées. 2) Le taux d'agression diminuait lorsque la densité des parcelles augmentait ; cette diminution était plus faible lorsque les parcelles n'étaient pas signalées que lorsqu'elles l'étaient. Cependant, contrairement aux deux prédictions, et donc contrairement aux modèles économiques de défense des ressources, les changements dans le taux d'agression ne résultaient pas de variations de l'agressivité individuelle, mais plutôt de variations du taux de rencontre entre individus. Par conséquent, la densité des parcelles ainsi que la connaissance de la localisation des parcelles n'ont pas influencé l'agressivité individuelle des moineaux domestiques. Cela met en question le rôle de ces deux facteurs dans les modèles économiques de défense des ressources.

Mots-clés: agression, approvisionnement social, cleptoparasitisme, défense des ressources, *Passer domesticus*

GENERAL INTRODUCTION

Group foraging is a common pattern of animal behaviour. However, group membership entails important foraging costs resulting from competition within the group. Namely, animals often take advantage of opportunities to eat food discovered by others. This exploitative social foraging behaviour is termed kleptoparasitism (*sensu* Giraldeau & Caraco 2000), given that it involves parasitically exploiting the investment of others. When food is divisible, this phenomenon can take the form of either scramble kleptoparasitism, which involves peaceful competitive scrambles for a share of the food discovered by another, or aggressive kleptoparasitism, which involves the use of force to gain exclusive access to the food (Giraldeau & Caraco 2000). Aggressive behaviour in the context of competition for a potentially limiting resource falls under the broad category of competitive aggression (*sensu* Archer 1988), which varies widely in form, from intimidating displays and threats to actual fights.

An individual's varied use of scramble versus aggressive kleptoparasitism begets behavioural flexibility in aggressiveness (i.e., the likelihood that aggression will occur, given an encounter with a competitor) and intraspecific variation in the frequency with which aggression occurs in foraging groups. For instance, Japanese medaka fish (*Oryzias latipes*) foraging in groups increase their level of aggressiveness as the clumping of food increases in space and decreases in time (Robb & Grant 1998). Indeed, a variety of animal taxa, including fish (Magnuson 1962; Rubenstein 1981; Grant & Kramer 1992; Grant & Guha 1993; Grand & Grant 1994; Bryant & Grant 1995; Ryer & Olla 1995; Robb & Grant 1998; Grant et al. 2002), birds (Zahavi 1971; Pimm 1978; Caraco 1979; Rohwer & Ewald 1981; Armstrong 1991; Kotrschal 1993; Saino 1994; Triplet et al. 1999; Goldberg et al. 2001; Dubois & Giraldeau 2004; Johnson et al. 2004, 2006), mammals (Monaghan & Metcalfe 1985; Isbell 1991), and insects (Hart 1986) exhibit variable amounts of aggression depending on ecological conditions. However, despite the numerous studies reporting intraspecific variation in aggression, there remain many unanswered questions regarding the ecological determinants of the level of aggressiveness in a kleptoparasitic setting.

Theoretical Models of Competitive Aggression

Two theoretical approaches provide frameworks for exploring the ecological determinants of competitive aggression: a simple optimality approach and a game theoretic approach. The models formulated using these approaches, collectively referred to as models of economic resource defence, predict that individual aggressiveness depends on the relationship between the costs and benefits of defence, and that being aggressive is only advantageous when the net benefits of defence are greater than the net benefits of non-aggressive competitive scrambles for food.

The simple optimality approach, encompassed in a body of literature collectively referred to as resource defence theory (reviewed by Grant 1993), evaluates the economic defendability (*sensu* Brown 1964) of resources; that is, the relationship between the net benefits of defence and the net benefits of non-aggressive tactics. Resource defence theory predicts that defensive behaviour, and hence individual aggressiveness, is contingent on a resource's economic defendability, thought to be influenced by several ecological parameters, namely, competitor density and at least five aspects of resource distribution in space and time: resource density (i.e., mean amount or mean production per unit area), spatial clumping (i.e., variance in density over space), temporal clumping (i.e., variance in density over time), spatial predictability (i.e., dependability of good and poor sites over time), and temporal predictability (i.e., dependability of good and poor times over space) (Emlen & Oring 1977; Warner 1980; Myers et al. 1981; Davies & Houston 1984; reviewed by Grant 1993). Resources typically considered in this context include mates, mating opportunities, space/shelter, and food. Originally, resource defence theory was aimed at investigating the occurrence of territoriality (see Brown 1964; Myers et al. 1981; Davies & Houston 1984), but it also often accurately predicts the occurrence of competitive aggression at smaller scales, such as the defence of ephemeral resource patches (see Grant 1993).

The game theoretic approach to the study of competitive aggression is aimed at predicting the occurrence of escalated fighting within populations (Maynard Smith & Price 1973; Maynard Smith 1982; Sirot 2000; Dubois et al. 2003). In hawk-dove games, the

archetype of this approach, animals can adopt one of two tactics: "hawk" which escalates aggressively, or "dove" which does not escalate and retreats in the face of aggression. The model determines the evolutionarily stable strategies (i.e., strategies which if adopted by a population cannot be invaded by any alternative; ESSs) of a population under different sets of ecological conditions (Maynard Smith & Price 1973). The aggressive hawk can exist as a pure ESS under some conditions, whereas the nonaggressive dove can only exist as part of a mixed ESS in which the frequency of hawk, and hence the proportion of encounters resulting in aggression, depends on the costs and benefits of escalated fighting. In other words, the model predicts that the aggressiveness of individuals within a population depends on the relationship between the cost of losing and the value of winning an aggressive interaction. Like resource defence theory, such game theoretic models predict that aggressiveness is contingent on several ecological factors, such as competitor density, resource patch density (i.e., the number of resource patches in a given area) and patch richness (i.e., the number of resource items in a given patch).

Effect of Knowledge of Patch Location on Aggression

One potential ecological determinant of aggressiveness, proposed only recently, has received little attention in the scientific literature: the foragers' certainty about the location of food patches (Dubois & Giraldeau 2004). Resource defence theory provides a framework for making predictions, given that whether or not an individual is informed of patch location may affect the size of the range that it needs to occupy in order to secure access to food, which in turn may affect the food's economic defendability. When patch location is known, an animal can obtain food while restricting its activities to a small, stable range; whereas when patch location is unknown, an animal must move about searching over a larger range in order to secure food. Given that the costs of defence are thought to increase with area (Schoener 1983), large ranges are less economically defendable, and therefore less likely to be defended than small ranges (Grant et al. 1992). Hence, resource defence theory predicts that aggressiveness should be higher when foragers know patch location than when they must search. Only one empirical study to date provides direct support for this prediction: Dubois &

Giraldeau (2004), in an experimental test using captive nutmeg mannikins (*Lonchura punctulata*), found a higher intensity (i.e., ranking of aggressive behaviour patterns on the basis of associated time and energy costs) and frequency of aggressive interactions among birds informed of patch location than among uninformed birds.

Indirect support for the prediction is provided by empirical studies that examine the effect of the spatial predictability of resource patches on aggression. Whether or not patches are spatially predictable is akin to whether or not foragers are informed of patch location, in that both factors potentially affect the size of the range foragers need to occupy in order to secure access to food (Dubois & Giraldeau 2004). Spatial predictability is defined as the degree to which good and poor resource patches are consistent over time, and it is usually measured by ranking patches in terms of resource density and measuring the correlation between these rankings over successive time intervals. A high positive correlation coefficient indicates a spatially predictable environment; in other words good patches are consistently good and poor patches are consistently poor (Warner 1980). Resource defence theory predicts that aggressiveness should be highest in spatially predictable environments because foragers can obtain food while restricting their activities to smaller and thus more economically defendable ranges. Unanimous support for this prediction is provided by the few empirical studies that explore the effect of spatial predictability on aggressive behaviour. Pimm (1978) and Rubenstein (1981) simultaneously manipulated the spatial predictability and spatial clumping of food, and monitored the defensive behaviour of three hummingbird species (*Archilochus alexandri, Eugenes fulgens, Lampornis clememciae*) and pygmy sunfish (*Elassoma evergladei*), respectively. Both studies found increased defensive behaviour with increased spatial predictability; however, the results are confounded by the fact that both spatial predictability and clumping were manipulated at the same time. Grand & Grant (1994), however, manipulated spatial predictability independently of all other aspects of resource distribution, and showed that dominant convict cichlids (*Cichlasoma nigrofasciatum*) were more aggressive when food was more spatially predictable. Hence, given that the spatial predictability of patches and foragers' knowledge of patch location are thought to affect aggression by similar means, these three studies provide indirect support for

the prediction that aggressiveness should be higher when foragers know patch location than when they must search.

Effect of Patch Density on Aggression

An ecological determinant of aggressiveness that has received much attention in the scientific literature is food patch density. Game theoretic models of resource defence predict a monotonic decline in aggressiveness with increasing patch density (Sirot 2000; Dubois et al. 2003). Such models assume that defending a challenged patch and searching for an alternative to replace a challenged patch are both costly in time and energy (Broom & Ruxton 1998; Sirot 2000; Dubois et al. 2003). As patch density increases, the cost of finding an alternative patch declines because more patches are concurrently available in the habitat and so finding an equivalent replacement patch is easier. Accordingly, the frequency of aggressive individuals (i.e., hawks) should decrease with increasing patch density; when the frequency of hawks decreases, the frequency of doves increases, as do interactions with doves, and therefore the proportion of encounters resulting in aggression declines.

A number of empirical studies (Magnuson 1962; Hart 1986; Armstrong 1991; Kotrschal et al. 1993; Triplet et al. 1999; Dubois & Giraldeau 2004) find evidence in support of a decrease in aggression with increasing food density. In particular, many investigations of birds foraging in shared patches seem to support this hawk-dove game prediction (see Sirot 2000). Furthermore, several studies (Zahavi 1971; Rohwer & Ewald 1981; Monaghan & Metcalfe 1985; Grant & Guha 1993; Ryer & Olla 1995; Robb & Grant 1998; Goldberg et al. 2001) show an increase in aggression when resources are more spatially clumped. Given that increasing spatial clumping may result in a reduction in patch density by increasing patch richness, the results of these studies may provide some support for the prediction of increased aggression with a reduction in patch density, even though it is clearly impossible to disentangle the effect of patch density from patch richness. The results of some empirical studies (Caraco 1979; Saino 1994), however, fail to support the game theoretic prediction. For instance, in a field experiment in which flocks of carrion crows (*Corvus corone corone*)

foraged on seeds artificially provided over a broad range of densities, Saino (1994) found that the frequency of aggressive encounters was independent of food density. Hence, even though much empirical evidence seems to uphold the game theoretic prediction, some evidence is to the contrary.

Effect of Patch Density as a Function of Knowledge of Patch Location

In an attempt to address the aforementioned mismatch between some empirical evidence and the game theoretic prediction of decreasing aggressiveness with increasing patch density, Dubois & Giraldeau (2004) hypothesize that whether or not foragers are informed of patch location should influence the effect of patch density on aggressiveness. When foragers know patch location, aggressiveness should decrease with increasing patch density, in accordance with theoretical expectation, because finding a replacement patch becomes cheaper (Sirot 2000; Dubois et al. 2003); whereas when foragers do not know patch location, aggressiveness should remain more-or-less unchanged with increasing patch density due to uncertainty about the availability and hence cost of finding a replacement patch. Dubois & Giraldeau (2004) point out that a gap in the literature currently exists seeing as most studies investigating the influence of food distribution on aggression presented food in such a manner that the foragers knew food location. For instance, in some studies (Monaghan & Metcalfe 1985; Grant & Kramer 1992; Goldberg et al. 2001; Johnson et al. 2004, 2006) food was offered in a very obvious manner such that its location was apparent to all foragers with very little search effort. In other studies (Grant & Guha 1993; Grand & Grant 1994; Robb & Grant 1998; Grant et al. 2002), food items were simply presented at a particular time interval or in particular locations, making search unnecessary. If Dubois & Giraldeau's (2004) hypothesis regarding the importance of foragers' certainty about the availability of replacement patches is correct, then when foragers are not informed of patch location, changing patch density should have little effect on aggressiveness.

In an experimental test using captive nutmeg mannikins, Dubois & Giraldeau (2004) provide the only empirical support to date for their hypothesis; as predicted, when the

mannikins were not informed of patch location, the frequency of aggression remained unaffected by patch density, and when the mannikins were informed, the frequency of aggression decreased with increasing patch density. However, as several authors (Grant & Kramer 1992; Grant & Guha 1993; Grand & Grant 1994; Robb & Grant 1998; Grant et al. 2002) point out, a decrease in the frequency of aggression does not necessarily involve behavioural flexibility in aggressiveness as is expected by the underlying game theoretic models of resource defence. A decrease in the frequency of aggression could be brought about by a decrease in the encounter rate between individuals of unchanged aggressiveness. Dubois & Giraldeau (2004), in fact, find no decrease in the intensity of aggressive interactions with increasing patch density, suggesting that the mannikins' aggressiveness may have remained unchanged, contrary to the game theoretic models on which they base their hypothesis. They argue that this failure to detect a decrease, however, could be ascribed to low statistical power resulting from small sample sizes. Notwithstanding, the support Dubois & Giraldeau (2004) provide for their hypothesis is debatable.

Objective and Predictions of the Present Study

In the present study, we test Dubois & Giraldeau's (2004) hypothesis attempting to disentangle whether the frequency of aggression changes as a result of a change in the encounter rate between individuals or as a result of a genuine change in the individual's level of aggressiveness. In other words, we used a better indicator of aggressiveness, by controlling for the encounter rate between individuals, and we tested their two predictions: 1) whether aggressiveness is higher when foragers know the location of food patches, and 2) whether the effect of patch density on aggressiveness depends on whether or not patch location is known. Our study tested Dubois & Giraldeau's (2004) predictions in a new light, using a different test species, namely the house sparrow (*Passer domesticus*, *Passeridae*, Passeriformes), foraging in larger groups, in a free-living rather than captive setting, and in a habitat offering more potential patch locations. As such, our study evaluates Dubois & Giraldeau's (2004) hypothesis under a different set of circumstances and thereby examines the robustness and predictive power of the underlying models of economic resource defence. House sparrows

are a good test species because they are known to adjust their aggressiveness in response to ecological change (i.e., competitor density and patch size: Johnson et al. 2004); moreover, they are highly sedentary (Summers-Smith 1988; Lowther & Cink 1992), permitting training of a wild population to recognize an experimentally provided signal of food patch location. If Dubois & Giraldeau's (2004) hypothesis regarding the importance of foragers' knowledge of patch location is correct, then 1) the frequency of aggression and aggressiveness should be higher when patch location is signalled than when it is not, and 2) the effect of patch density on the frequency of aggression and on aggressiveness should depend on whether or not patch location is signalled; that is, when location is signalled, aggression should decrease with increasing patch density, but when location is not signalled, aggression should remain more-or-less unchanged with increasing patch density.

AGGRESSION WHEN FACED WITH UNCERTAINTY: AN EXPERIMENTAL TEST USING WILD FORAGING HOUSE SPARROWS (*PASSER DOMESTICUS*)

PHOENIX BOUCHARD-KERR AND LUC-ALAIN GIRALDEAU

Département des sciences biologiques, Université du Québec à Montréal

Running headline : Aggression & uncertainty. Bouchard-Kerr & Giraldeau.

ABSTRACT

When foraging in groups, whether animals know the location of food patches is thought to influence both 1) their level of aggressiveness and 2) how aggressiveness changes as a function of patch density. 1) Resource defence theory predicts that an animal's aggressiveness should be greatest when it knows patch location and can therefore limit its search to a smaller, more economically defendable area. 2) Game theoretic models predict that aggressiveness should decrease with increasing patch density because replacement patches become more readily available; however, when patch location is unknown, aggressiveness should remain more-or-less unchanged with increasing patch density due to uncertainty about the availability of replacement patches. We experimentally tested these predictions using flocks of wild house sparrows. We simultaneously manipulated patch density and whether or not patch location was signalled. Changes in the frequency of aggressive interactions seemingly provided support for both predictions. 1) Aggression occurred most frequently when patch location was signalled. 2) The frequency of aggression decreased to a lesser extent with increasing patch density when patch location was not signalled. However, contrary to both predictions, and hence contrary to models of economic resource defence, changes in the frequency of aggression were not brought about by variation in the birds' level of aggressiveness, but instead by variation in the encounter rate between birds. Hence, for our house sparrows, both patch density and knowledge of food patch location are apparently inconsequential to individual aggressiveness, casting doubt on the role of these factors in models of economic resource defence.

INTRODUCTION

An animal's aggressiveness (i.e., the likelihood that aggression will occur, given an encounter with a competitor) is thought to be influenced by a number of ecological factors, such as competitor density, patch density and patch richness, to name a few. These ecological determinants are explored by models of economic resource defence, using either simple optimality (i.e., resource defence theory: Grant 1993) or game theoretic (i.e., hawk-dove games: Sirot 2000; Dubois et al. 2003) approaches. In such models, individual aggressiveness depends on the relationship between the costs and benefits of defence, such that aggression is only expected when the net benefits of defence are greater than the net benefits of competitive scrambles for food.

One potential ecological determinant of aggressiveness pertains to certainty about food patch location. Dubois & Giraldeau (2004) predict that whether or not foragers are informed of patch location influences both 1) the level of individual aggressiveness and 2) how individual aggressiveness changes as a function of patch density (i.e., the number of concurrent food patches in a given area).

The first prediction, based on resource defence theory, assumes that knowledge of patch location is akin to spatial predictability given that both may affect the size of the range a forager needs to defend in order to secure access to food. Aggressiveness should be highest in predictable environments because a forager can restrict its activities to a small, economically defendable (sensu Brown 1964) range; whereas, in unpredictable environments, a forager must search over a larger, less economically defendable range to obtain the same certainty of access to food (Warner 1980; reviewed by Grant 1993). Dubois & Giraldeau (2004) provide experimental support for this prediction, reporting a higher intensity and frequency of aggressive interactions among captive nutmeg mannikins (*Lonchura punctulata*) informed of patch location than among uninformed mannikins.

The second prediction states that foragers' certainty about patch location influences how patch density affects aggressiveness. Game theoretic models assume that both defending

a challenged patch and searching for an alternative patch as replacement are costly in time and energy (Broom & Ruxton 1998; Sirot 2000; Dubois et al. 2003). Accordingly, aggressiveness should decrease with increasing patch density because finding a replacement patch becomes cheaper (Sirot 2000; Dubois et al. 2003). However, when animals do not know the location of patches, they are uncertain about the availability and hence the cost of replacements, and so increasing patch density should have little effect on their aggressiveness (Dubois & Giraldeau 2004). In support of this prediction, Dubois & Giraldeau (2004) showed that when nutmeg mannikins were not informed of patch location, their frequency of aggression remained unaffected by patch density, but when informed, their frequency of aggression decreased with increasing patch density. However, several authors point out that a decrease in the frequency of aggression does not necessarily involve behavioural flexibility in aggressiveness, it could instead be brought about by a decrease in the encounter rate between individuals of unchanged aggressiveness (Grant & Kramer 1992; Grant & Guha 1993; Grand & Grant 1994; Robb & Grant 1998; Grant et al. 2002). Dubois & Giraldeau (2004), in fact, find no decrease in the intensity of aggressive interactions with increasing patch density, suggesting that aggressiveness may have remained unchanged. They argue that this failure to detect a decrease, however, could be ascribed to low statistical power resulting from small sample sizes. Notwithstanding, the support Dubois & Giraldeau (2004) provide for their second prediction is not as strong as it could be.

In the present study, we test Dubois & Giraldeau's (2004) two predictions, attempting to disentangle whether the frequency of aggression changes as a result of a change in the encounter rate between individuals or as a result of a genuine change in the individual's level of aggressiveness. We test their predictions in a new light, using a different test species, namely the house sparrow (*Passer domesticus*, *Passeridae*, Passeriformes), foraging in larger groups, in a free-living rather than captive setting, and in a habitat offering more potential patch locations. House sparrows are a good test species because they are known to adjust their aggressiveness in response to ecological change (i.e., competitor density and patch size: Johnson et al. 2004); moreover, they are highly sedentary (Summers-Smith 1988; Lowther & Cink 1992), permitting training of a wild population to recognize an experimentally provided signal of food patch location. If Dubois & Giraldeau's (2004)

hypothesis regarding the importance of foragers' knowledge of patch location is correct, then 1) the frequency of aggression and aggressiveness should be higher when patch location is signalled than when it is not, and 2) when location is signalled, the frequency of aggression and aggressiveness should decrease with increasing patch density, but when location is not signalled, the frequency of aggression and aggressiveness should remain more-or-less unchanged with increasing patch density.

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METHODS

Study Site and Population

The study was conducted during winter 2004-2005 in a shaded courtyard on the northeast side of a three-story apartment building in urban Montréal, Québec, Canada. Shelter for the house sparrows was provided by six fresh-cut fir trees, ranging in height from 1.2-1.8 m. The number of house sparrows visiting the site was conservatively estimated as at least 31 birds, since this was the most birds seen at once. Throughout December and early January we captured and individually marked birds using a baited pull-string trap and mist nets, but poor conditions resulted in the capture and marking of only six females and three males. European starlings (*Sturnus vulgaris*), grey squirrels (*Sciurus carolinensis*) and feral pigeons (*Columba livia*) were often seen in the vicinity of the site, and so another feeding station was provided nearby in an open area little frequented by house sparrows to keep heterospecific intruders away.

Experimental Apparatus and Procedure

The feeding table, a 1.0 x 1.0 m plywood board with a wooden rim rising 2.0 cm above its perimeter, was positioned 25 cm from the ground and 2.0 m from the nearest fir tree. The table held an array of 16 round terracotta seed dishes (15 cm diameter opening and 2.2 cm depth) arranged in four rows of four, with each dish placed at a 25 cm interval from the centre of neighbouring dishes. All dishes contained a double layer of dried yellow peas, and randomly selected dishes each contained 50 white millet seeds hidden under the peas. Consequently, in order to detect and gain access to food, the house sparrows had to root through the peas.

In a two-factor experimental design, we manipulated signal (i.e., the presence of a colour-signal indicating which dishes contained millet) and patch density (i.e., the total number of dishes containing millet). The signal factor had two levels: with or without signal.

The patch density factor had three levels: low, medium or high density, in which 3/16, 6/16 or 9/16 dishes contained millet. In the with-signal environment, dishes containing millet were red, and dishes without millet were white. In the without-signal environment, all dishes were blue, regardless of whether or not they contained millet. Note that every day from January 31st to February 28th from 0730 h to 1230 h (EDST) the birds foraged in with- and without-signal environments, with the objective of training the house sparrow population to recognize that only red dishes contained food in the with-signal environment and that any dish could contain food in the without-signal environment.

Trials were conducted every day from March 2nd to 19th and videotaped using a digital video camera mounted on a tripod from behind a window located 1.4 m from the board. Each day the birds experienced all six signal x density conditions in random order for six consecutive trials. A trial started when the first bird initially arrived on the board and ended at the moment from which point onward there were fewer than six birds on the board for at least 45 consecutive seconds. A condition was considered improperly tested when a trial: 1) ended before all food patches were discovered; and/or 2) fewer than six birds were simultaneously present on the board for more than 30% of the total trial duration, omitting any time when there were no birds on the board (i.e., short periods of 45 s or less). An additional trial for each improperly tested condition was conducted after the first six trials of the day. This process of trial repetition was reiterated throughout the day in an attempt to complete one properly tested trial for each of the six conditions. A mean of 13 (range 8-19) trials were conducted per day, from 0730 h onwards, recording the time of day at the onset of each trial, and the ambient temperature to the nearest 1°C using a thermometer located 1.5 m from the board. After the last trial of the day, the dishes were removed and more than enough millet seeds were spread on the board to feed the house sparrow population for the remaining day-light hours.

Observations

Data were collected from the 6th day of trials onwards via playbacks of the videotapes, using Videopro software and The Observer event recording software, both from Noldus Information Technology, Wageningen, The Netherlands. The following definitions were used: a food patch (i.e., a dish containing millet) was discovered when a bird's beak first touched the peas in the dish; a bird was at a given food patch when its beak was located over the dish's lip and/or the bird itself was standing on the dish; an encounter occurred whenever a bird arrived at a food patch already attended by one or more birds (the total number of encounters multiplied by the number of birds present at the patch upon the bird's arrival); an aggressive interaction was defined as any aggressive act ranging from wing flapping to escalated fighting, the intensity of each aggressive interaction scored from 1 to 5 on the basis of associated energetic and time costs as well as risk of injury (after Johnson et al. 2004; Lowther & Cink 1992) (see Table 1 for definitions used for scoring).

Observations were conducted at two spatial scales: at the level of the whole board and at the level of a single food patch. At the board level, the observer (P.B.K.) used continuous recording to note the times at which each food patch was discovered and the times at which the number of birds on the board changed prior to the discovery of the last food patch. Scan sampling (with 5 s observation periods at 15 s intervals) was used for the entire trial duration to record the times at which the number of birds on the board changed, and the occurrence and intensity of all aggressive interactions. At the patch level, the observer used continuous observation of the third food patch discovered, from its discovery until the end of the trial, to record the times at which the number of birds attending the patch changed, the occurrence of all encounters, and the occurrence and intensity of all aggressive interactions between birds at the patch.

Table 1. Intensity scores assigned to aggressive behaviour patterns of the house sparrow (*P. domesticus*) on the basis of associated energetic and time costs as well as risk of injury (modified from Johnson et al. 2004; after the method of Lowther & Cink 1992).

Intensity	Behaviour pattern
1	Wing flapping in the presence of opponent, often with beak open; no physical contact
2	Hopping or lunging towards opponent, often with beak open; no physical contact
3	Pecking (i.e., physical contact via beak) opponent one to three times
4	Lunging and landing on opponent while pushing with legs and pecking opponent one to three times
5	Escalated fighting in which both opponents stand in upright positions with erected chest feathers and engage in four or more reciprocal pecks with wing flapping.

Data Analysis

Since too few individual birds were banded and thus recognizable, we based our statistical analyses on group measures for a given trial as an individual data point (as per Johnson et al. 2004). Hence, trials for each condition retested on successive days were considered replicates. This method dealt with the problem of lack of independence between individual behavioural observations (Johnson et al. 2004; Lima 1992), since all trials likely differed from one another in terms of group composition, given the fluctuations in the number of birds visiting the study site as well as the frequent changes in the number of birds on the board and at a food patch during a trial.

For each trial the number of birds observed was weighted by the cumulative time spent foraging at that number. We calculated the mean weighted number of birds both on the board and at a food patch per trial (omitting all times when there were no birds either on the board or at the patch, respectively). We estimated the per capita rate of patch discovery (patches/min/bird) for each trial as the number of patches discovered, divided by the time interval from the start of the trial to the discovery of the last patch, divided by the trial's mean weighted number of birds on the board for that interval. At both the board and patch level, for each trial we estimated: 1) the total rate of aggression (interactions/min), omitting all times when there was less than two birds on the board, 2) the per capita rate of aggression (interactions/min/bird), as the total rate of aggression divided by the mean weighted number of birds, and 3) aggressive intensity, as the mean intensity score per trial calculated using all aggressive interactions. To quantify the opportunity for aggression at the patch level, we calculated the encounter rate (encounters/min). To quantify aggressiveness at the patch level, we calculated the percentage of encounters resulting in aggression, as the number of aggressive interactions occurring within 3 s of an encounter divided by the total number of encounters.

Group measures tabulated for each trial were submitted to two-factor full factorial (i.e., signal, density, and signal x density) analysis of variance (ANOVA), conducting post-hoc pair wise comparisons using Tukey's HSD test. To test our first prediction, we used

board level analyses of aggression, since this level alone included aggressive interactions between birds searching for food patches. To test our second prediction, we used patch level analyses of aggression, since a food patch was a defendable unit. Temperature and time of day may affect levels of aggression in house sparrow groups (Barnard 1981), consequently, analysis of covariance (ANCOVA) models were used to test for the effects of these variables on the total and per capita rates of aggression, aggressive intensity, and aggressiveness. We could thereby control for the effects of significant covariates, and non-significant covariates could be removed from the models. ANCOVA models were also used to test and control for the effect of encounter rate on patch level per capita rate of aggression, as an additional method for assessing the opportunity for aggression and aggressiveness. All statistical analyses were conducted using JMP version 5.0, SAS Institute, Cary, North Carolina. When necessary, data were transformed to satisfy the conditions of application for parametric analyses. All results are expressed as means with standard error of untransformed data.

RESULTS

General

We conducted 48 trials during the five day familiarization period, and 180 trials during the 13 day experimental period, of which 71 trials were used for data collection (Table 2). The first house sparrow landed on average 62 ± 12 s after the feeding table had been replenished, with several birds usually arriving in close succession. A trial lasted 178.9 ± 5.6 s, with the number of birds on the board (range = 1 -19) changing every 6.6 ± 0.5 s, and the number of birds at a food patch (range =1 - 4) changing every 11.7 ± 1.2 s.

Most aggressive interactions occurred at food patches rather than elsewhere on the board, and involved no physical contact between the two opponents (i.e., intensity score of 1 or 2; Table 3). The birds learned to recognize the red colour-signal of dishes containing food, as evidenced by a significantly faster per capita rate of patch discovery when food location was signalled than when it was not, in both low and high patch density conditions (Tukey: $P < 0.05$), despite a significant interaction between signal and patch density (ANOVA on log-transformed data: $F_{2,65} = 5.04$, $P = 0.0092$) (Fig. 1).

Table 2. Number of trials, for each signal x density condition, conducted during the familiarization and experimental periods, as well as the number of experimental period trials that were deemed properly tested and thus used for data collection.

Signal	Patch density	Period	Trials conducted	Trials used for data collection
With	Low	Familiarization	9	–
		Experimental	29	10
With	Medium	Familiarization	7	–
		Experimental	29	12
With	High	Familiarization	8	–
		Experimental	29	13
Without	Low	Familiarization	8	–
		Experimental	35	12
Without	Medium	Familiarization	7	–
		Experimental	31	11
Without	High	Familiarization	9	–
		Experimental	27	13

Table 3. Percentage (and fraction) of aggressive interactions receiving intensity scores 1 through 5, for house sparrows observed at either the board or patch level. See Table 1 for definitions used for scoring.

Intensity	Level of observation	
	Board	Patch
1	31.4% (302/961)	18.0% (77/427)
2	48.8% (469/961)	55.5% (237/427)
3	16.0% (154/961)	22.7% (97/427)
4	2.6% (25/961)	3.0% (13/427)
5	1.1% (11/961)	0.7% (3/427)
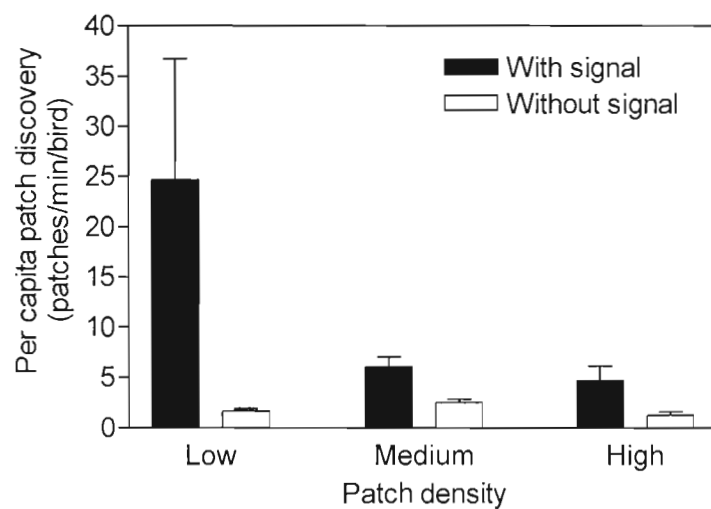
Figure 1. Mean (+ SE) per capita rate of patch discovery of the house sparrows in relation to patch density and whether or not food patch location was signalled.

The mean weighted number of birds on the board during a trial was unaffected by signal (ANOVA: $F_{1,65} = 0.40$, $P = 0.53$) but increased significantly with patch density (ANOVA: $F_{2,65} = 5.00$, $P = 0.0096$), post-hoc pair wise comparisons significant only between low (8.25 ± 0.25 birds) and medium (9.35 ± 0.34 birds), and between low and high patch densities (9.44 ± 0.26 birds; Tukey: $P < 0.05$). There was no interaction between signal and patch density on the mean weighted number of birds on the board (ANOVA: $F_{2,65} = 0.11$, $P = 0.89$).

For the mean weighted number of birds at a food patch, there was an interaction between signal and patch density (ANOVA: $F_{2,65} = 4.36$, $P = 0.017$). Post-hoc pair wise comparisons reveal that the number of birds at a food patch was significantly higher in the with-signal than in the without-signal condition when patch density was low (with-signal: 1.54 ± 0.08; without-signal: 1.21 ± 0.06; Tukey: $P < 0.05$), but not when it was medium or high. Furthermore, the number of birds at a food patch decreased significantly between low (1.54 ± 0.08 birds) and high patch densities (1.16 ± 0.05 birds; Tukey: $P < 0.05$) when food location was signalled, but no pairs of patch density levels were significantly different when food location was not signalled.

Ambient temperature (range = -15°C to 1°C) and time of day (i.e., start time of trial, range = 0808h to 1650h) did not significantly affect total nor per capita rates of aggression at neither the board nor patch level, nor did it affect patch level aggressive intensity (ANCOVA: $P > 0.074$). Hence, ambient temperature and time of day were omitted from these analyses. Board level aggressive intensity decreased with increasing temperature (ANCOVA: $F_{1,64} = 7.28$, $P = 0.0089$), and aggressiveness (i.e., the percentage of encounters resulting in aggression at the patch level) increased with time of day (ANCOVA: $F_{1,64} = 11.67$, $P = 0.0011$) and temperature (ANCOVA: $F_{1,64} = 9.57$, $P = 0.0029$). Notwithstanding, the results of these ANCOVA models were qualitatively similar to those of the corresponding ANOVA models, so below we report only the latter. ANOVA results for total rate of aggression were qualitatively similar to those for per capita rate of aggression (both at the patch and board level), so below we report only the later.

Prediction 1: Is aggression higher when food location is signalled?

Board level per capita rate of aggression was significantly higher when food location was signalled than when it was not (ANOVA: $F_{1,65} = 6.00$, $P = 0.017$; Fig. 2a), however board level aggressive intensity was not affected by signal (ANOVA: $F_{1,65} = 0.18$, $P = 0.68$; Fig. 2b). In both cases, there was no interaction between signal and patch density (ANOVA: $F_{2,65} = 0.46$, $P = 0.64$; $F_{2,65} = 0.22$, $P = 0.80$).

Prediction 2: Is patch density's effect on aggression dependent on signal?

The effect of patch density on patch level per capita rate of aggression depended on signal (ANOVA: $F_{2,65} = 3.64$, $P = 0.032$). Visual inspection of our results suggests that aggression decreased to a lesser extent with increasing patch density when food location was not signalled (Fig. 3a). Indeed, post-hoc pair-wise comparisons reveal that when food location was not signalled, aggression decreased significantly only between low and high patch densities (Tukey: $P < 0.05$), whereas when food location was signalled, aggression decreased significantly not only between low and high patch densities, but also between low and medium patch densities (Tukey: $P < 0.05$).

The effect of patch density on encounter rate (i.e., the opportunity for aggression) depended on signal (ANOVA on square-root-transformed data: $F_{2,65} = 4.29$, $P = 0.018$). Visual inspection of our results suggests that encounter rate decreased to a lesser extent with increasing patch density when food location was not signalled (Fig. 3b). Indeed, post-hoc pair wise comparisons did not reveal any significant difference between the three patch density levels when food location was not signalled; but when food location was signalled, encounter rate decreased significantly between both low and medium, and low and high patch densities (Tukey: $P < 0.05$).

Aggressiveness (Fig. 3c) and patch level aggressive intensity (2.15 ± 0.06) were not significantly affected by signal (ANOVA: $F_{1,65} = 1.09$, $P = 0.30$; $F_{1,65} = 0.27$, $P = 0.60$) nor

patch density (ANOVA: $F_{2,65} = 0.064$, $P = 0.94$; $F_{2,65} = 0.76$, $P = 0.47$), and there was no interaction between the two factors (ANOVA: $F_{2,65} = 1.00$, $P = 0.37$; $F_{2,65} = 0.56$, $P = 0.57$). Furthermore, when we tested and controlled for the effect of encounter rate on patch level per capita rate of aggression, aggression increased with encounter rate (ANCOVA on square-root-transformed data: $F_{1,64} = 82.48$, $P < 0.0001$), there was no effect of signal (ANCOVA: $F_{1,64} = 0.0005$, $P = 0.98$), nor patch density (ANCOVA: $F_{2,64} = 1.84$, $P = 0.17$), and no interaction between the two factors (ANCOVA: $F_{2,64} = 0.16$, $P = 0.85$).
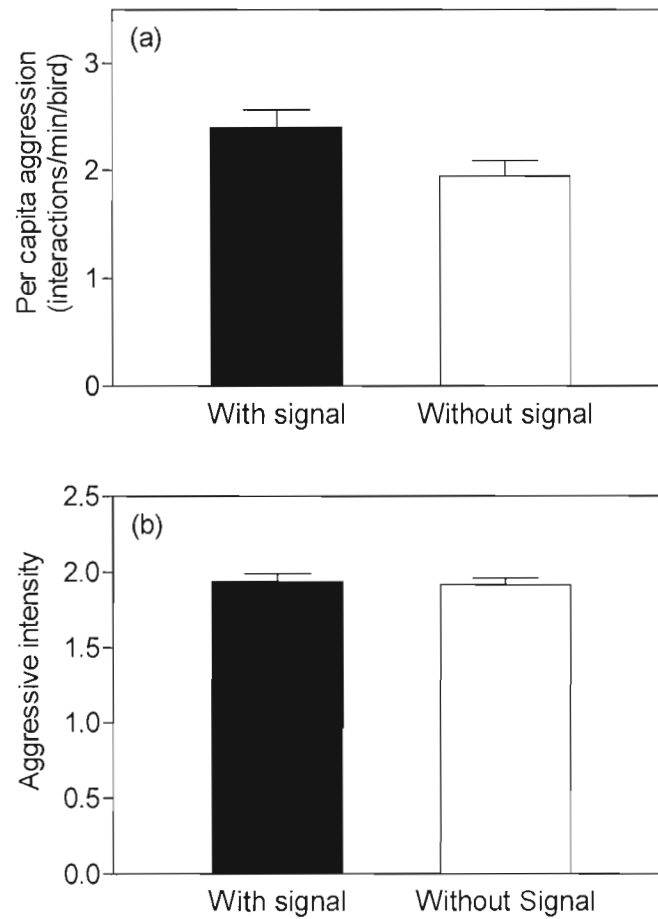
Figure 2. Mean (+ SE) board level per capita rate of aggression (a) and aggressive intensity (b) of the house sparrows when food location was either signalled or not signalled. Data for the three patch density levels were pooled to estimate the means.
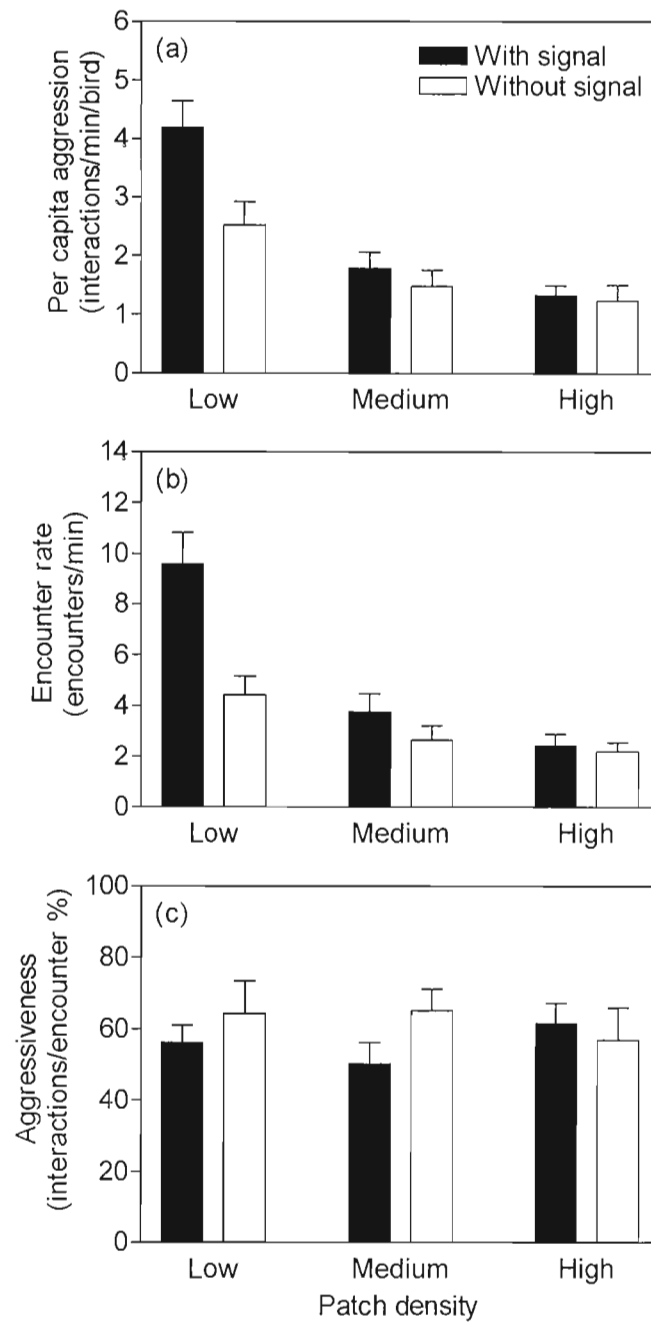
Figure 3. Mean (+ SE) patch level per capita rate of aggression (a), encounter rate (b) and aggressiveness (c) of the house sparrows in relation to increasing patch density when food location was either signalled or not signalled.

DISCUSSION

Patterns of change in the frequency of aggression among our foraging house sparrows seemingly provide support for both of Dubois & Giraldeau's (2004) predictions: 1) aggression occurred most frequently when food location was signalled, and 2) the effect of patch density on the frequency of aggression depended on signal. However, our analyses reveal that these changes in the frequency of aggression were not brought about by variation in the birds' level of aggressiveness, but instead by variation in the encounter rate between birds. Consequently, we show that relying solely on the frequency of aggression to test the predictions can be misleading; once we take into account our birds' aggressiveness, we find no support for the two predictions. We discuss the implication of these results for each prediction in turn.

Prediction 1: Effect of Knowledge of Patch Location

The frequency of aggression among house sparrows foraging on the board was higher when food location was signalled than when it was not. We thereby corroborate Dubois & Giraldeau's (2004) finding that aggression in captive nutmeg mannikins occured most frequently when food location was signalled. Moreover, we corroborate studies that document a higher frequency of aggression when food was more spatially predictable (Pimm 1978; Rubenstein 1981; Grand & Grant 1994). However, our house sparrows' higher frequency of aggression was not paralleled by higher aggressive intensity. Therefore, contrary to the expectations of resource defence theory, the increase in aggression probably did not arise via an increase in the birds' aggressiveness, but rather by an increase in the encounter rate between birds on the board.

Our rejection of the first prediction, however, is tempered by potential limitations of our experiment. On the one hand, the without-signal environment might not have forced the birds to search over a much larger, less economically defendable range than the with-signal

environment. Despite having to invest some effort in searching in the without-signal environment, the birds may have uncovered food patches so quickly that the size of the range occupied was similar to that in the with-signal environment. One might argue that if we had provided a without-signal environment that forced the birds to search more extensively for food, we would have observed an effect of signal on aggressiveness. However, we believe this is unlikely because our treatment did induce a change in the per capita rate of food patch discovery in the desired direction, and we nonetheless did not detect even the slightest increase in aggressive intensity, and hence aggressiveness.

In another potential limitation of our experiment, perhaps the house sparrows lacked flexibility in the size of area they will defend. The birds we studied may have been unwilling or unable even to attempt to defend large areas. The house sparrows fought mostly with their closest neighbours, a behaviour that is consistent with reports by Johnson et al. (2004), whose house sparrows, while foraging in a patch of visible seeds, also only fought with immediate neighbours rather than attempting to defend larger areas. Johnson et al. (2004) nonetheless suggest that the house sparrow can adjust aggressiveness in response to food patch size; however, their experimental evidence hinges on an indicator of aggressiveness that does not control for competitor encounter rate and in addition they fail to find a change in aggressive intensity. Future tests of this prediction should perhaps use a species that exhibits greater flexibility in the size of the area it will defend, because without such prior assurance it is impossible to decide whether the prediction is truly rejected.

Prediction 2: Effect of Patch Density as a Function of Knowledge of Patch Location

The effect of patch density on the frequency of aggression among house sparrows foraging at a food patch depended on signal: aggression decreased to a lesser extent with increasing patch density when food patch location was not signalled. Our results thereby corroborate Dubois & Giraldeau's (2004) report of an interaction between the effect of patch density and signal on the frequency of aggression. However, the nature of our study's interaction differs from the interaction reported for the nutmeg mannikins; in the mannikins'

without-signal condition, aggression remained unchanged rather than decreasing with increasing patch density. There are two possible non-exclusive explanations for this difference. On the one hand, perhaps an effect of signal simply went undetected in the mannikin study because of insufficient statistical power resulting from small sample sizes. On the other hand, perhaps our study failed to withhold location information completely in the without-signal environment, accounting for the observed weak decrease in aggression with increasing patch density. The presence and/or behavioural activities of house sparrows at uncovered patches may have indicated food location in the without-signal environment; a possibility supported by abundant evidence in the scientific literature showing that animals often locate food using the presence and/or activities of others (Galef & Giraldeau 2001). In the without-signal environment of the mannikin study, presence of such information was much less likely because there were fewer (three) birds foraging simultaneously among the nine potential patch locations. Either or both of these explanations could account for the difference between the two studies' reported interaction.

Despite the house sparrows' probable use of social information on patch location in the without-signal environment, they apparently did not attain the same level of certainty about the availability of replacement food as in the with-signal environment. Consistent with this interpretation, we found that the birds experienced a lower per capita rate of patch discovery and fewer encounters at food patches in the without-signal environment, despite a similar total number of birds on the board. Our results suggest that this difference in certainty between signal conditions may have been sufficient to influence patch density's effect on the frequency of aggression, consistent with Dubois & Giraldeau's (2004) second prediction.

This apparent consistency with the second prediction, however, was not paralleled by changes in aggressiveness. The percentage of encounters resulting in aggression at the patch level did not vary significantly with patch density, even though the food patch we observed had the greatest potential for eliciting higher aggressiveness when patch density was low since it was the third, and hence last, food patch discovered. Instead, the house sparrows behaved according to a fixed rule: regardless of patch density, use aggression in about 60% of encounters with competitors when at the third food patch discovered. Furthermore, when

we statistically controlled for the effect of encounter rate with competitors on patch level per capita rate of aggression, aggression did not change with patch density. Finally, aggressive intensity did not vary significantly with patch density. All of these results are consistent with Dubois & Giraldeau's (2004) mannikins' lack of change in aggressive intensity, and hence aggressiveness, in response to patch density. While Dubois & Giraldeau (2004) attribute their failure to detect an effect to low statistical power, given the three lines of evidence we have just discussed, we are confident that the sparrows did not adjust their level of aggressiveness in response to patch density, at least not by an ecologically relevant magnitude. Alternatively, one might argue that the sparrows regulated the rate at which they encountered competitors in order to regulate the frequency at which they could be aggressive. In this sense, our observed decrease in encounter rate with increasing patch density could be interpreted as a decrease in aggressiveness. We believe however that this interpretation is inconsequential since the rate at which the birds encountered competitors was probably largely a product of patch distribution and thus independent of the birds' will. Nevertheless, the idea that an animal might regulate its encounters with competitors depending on its aggressiveness warrants future experimental testing. In the context of the present study, however, we conclude that our results reject Dubois & Giraldeau's (2004) second prediction since uncertainty about the availability of replacement food apparently had no impact on patch density's effect on aggressiveness.

Assuming that the house sparrow can adjust aggressiveness in response to patch density, the lack of change in aggressiveness may also have been due to the presence of a large number of alternative food patches. In such conditions, perhaps foragers have little to gain by adjusting aggressiveness, in spite of changes in patch density. We offered more than one concurrent food patch in all three levels of patch density; similarly, Dubois & Giraldeau (2004) offered more than one concurrent food patch in two out of the three levels of patch density. Hence, in both experiments an equivalent alternative patch was usually available to replace that which was lost to a rival, and so perhaps it was cheaper to uncover a replacement patch than to escalate aggressively. Indirect support for this line of reasoning is provided by Grant & Guha (1993) who manipulated the spatial clumping of food by varying the distance between three concurrent food patches, thereby providing replacements for lost patches, and

found unchanged aggressiveness among foraging convict cichlids (*Cichlasoma nigrofasciatum*). Whereas, Grant & Kramer (1992) who manipulated the temporal clumping of food at a single patch, thereby providing no replacement patches, found variation in aggressiveness among zebrafish (*Brachydanio rerio*) consistent with theoretical expectations. Clearly, explicit experimental testing is needed to determine if the presence of alternative patches has an impact on whether or not foragers' will alter their aggressiveness in response to ecological change. If our reasoning is correct, however, we predict little variation in foragers' aggressiveness when the distribution of food is patchy and replacement patches are readily available.

The game theoretic prediction of decreased aggressiveness with increasing patch density may actually be amiss, given that it is founded on a questionable assumption; namely, that individuals deciding whether or not to appropriate a food patch aggressively, face the same economic decision as individuals already occupying a food patch and deciding whether or not to defend aggressively against appropriators (Dubois & Giraldeau 2005). In a more recent game theoretic model, Dubois & Giraldeau (2005) incorporate the economics of both defence and appropriation, and suggest that the level of aggression in a group should depend mostly on the decision of appropriators. Like the aforementioned models (Sirot 2000; Dubois et al. 2003), the frequency of aggression is predicted to decrease with increasing patch density. However, in contrast to these models, the decrease in aggression is predicted to arise via a lower encounter rate between competitors whose level of aggressiveness remains virtually unchanged. In effect, the results of both our study and that of Dubois & Giraldeau (2004) are more consistent with the predictions of this game theoretic model of resource defence and appropriation.

Our results reveal that the encounter rate between birds at food patches, and hence the manner in which the birds distributed themselves among the food patches, was responsible for the patch density's effect on the frequency of aggression within each signal environment. When in the presence of a signal, the birds possessed perfect information about food patch availability; accordingly, the birds spread out among the food patches in a more-or-less ideal free distribution (Fretwell & Lucas 1970; reviewed by Giraldeau & Caraco

2000), and so our experimental increase of patch density increased the number of patches over which the birds could distribute themselves, resulting in fewer encounters at each patch and lower opportunity for aggression. Whereas, when in the absence of a signal, the birds only had access to imperfect information about food patch availability and accordingly, the birds searched for food and uncovered patches in a more sequential manner, regardless of patch density, and so increasing patch density had less effect on the number of encounters at each food patch. Thus, in our study, the frequency of aggression decreased with increasing patch density in both signal environments, albeit at different magnitudes, as the result of a reduced encounter rate between birds rather than a reduction in the birds' level of aggressiveness.

To conclude, the frequency of aggression among the house sparrows was lower and decreased to a lesser extent with increasing patch density when the birds were less certain about food patch location. These effects were attributable to a reduced encounter rate between individuals between conditions rather than to reduced individual aggressiveness. Consequently, we fail to find support for Dubois & Giraldeau's (2004) predictions concerning the importance of certainty about food location on aggressiveness and on how patch density affects aggressiveness. Our rejection of the predictions casts doubt on the importance of patch density and foragers' knowledge of patch location in models of economic resource defence. Further experiments are required to confirm this conclusion; namely it would be particularly relevant to use animals that can substantially alter their aggressiveness, and experimental environments that tax the searching costs of the animals while offering few alternative food patches. We predict that certainty about food location would be important under such conditions.

ACKNOWLEDGEMENTS

GENERAL CONCLUSION

The present study is the second to explore Dubois & Giraldeau's (2004) hypothesis concerning the importance of foragers' knowledge of patch location on aggressiveness and on how patch density affects aggressiveness. It is the first, however, to disentangle if patch density and knowledge of patch location do in fact bring about a change in the individual's level of aggressiveness, in accordance with the underlying game theoretic models of resource defence, or if these factors only affect the individual's opportunity to be aggressive.

The frequency of aggression among our house sparrows was lower and decreased to a lesser extent with increasing patch density when the sparrows were less certain about patch location. These effects were attributable to a reduced encounter rate among individuals between conditions rather than to reduced individual aggressiveness. Consequently, our results do not support Dubois & Giraldeau's (2004) two predictions: 1) aggressiveness was not significantly higher when the sparrows were more certain of patch location, and 2) aggressiveness was not significantly affected by patch density when the sparrows were more certain of patch location. We therefore demonstrate that, contrary to the expectations of models of economic resource defence, animals sometimes use a fixed behavioural rule instead of adjusting their aggressiveness.

Previous studies also find concrete evidence of animals exhibiting fixed aggressiveness in the face of ecological change, contrary to theoretical expectations (Grant & Guha 1993; Grant et al. 2002). In other studies, claims of a change in aggressiveness are potentially erroneous due to reliance on the frequency of aggression as an indicator of aggressiveness, without controlling for variation in the opportunity for aggression (Monaghan & Metcalfe 1985; Grant & Kramer 1992; Bryant & Grant 1995; Goldberg et al. 2001; Dubois & Giraldeau 2004). In light of our results, as well as those of these other studies, we propose that animals may sometimes act according to a fixed rule in the face of ecological change rather than adjusting their aggressiveness. If this is the case, then the predictive power of models of economic resource defence is limited.

In our study, the house sparrows' failure to adjust their aggressiveness may have ensued from a number of circumstances. Perhaps our birds did not have the capacity to alter their aggressiveness. Or perhaps our foraging environments were not conducive to flexibility in aggressiveness, due to the ease with which our birds found food patches or to the presence of ample replacements for patches lost to rivals. These potential limitations of our experiment temper our rejection of Dubois & Giraldeau's (2004) predictions and of the underlying models of economic resource defence. We therefore call for future experiments, testing animals that can substantially alter their aggressiveness, in foraging environments that are conducive to flexibility in aggressiveness, that is, environments that demand significant food-searching effort and that offer few alternative patches. Moreover, we insist that future tests follow our example by relying on a better indicator of aggressiveness than the frequency of aggression, given our experiment's demonstration that patch density and knowledge of patch location strongly affect competitor encounter rate and hence the opportunity for aggression.

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