

# Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove

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The spatial and temporal clumping of food influence an animal's aggressiveness during competition. No studies, however, have investigated the effects of the temporal predictability of food and few studies have tested for interactions between the effects of two components of resource distribution on the rates of competitive aggression. We simultaneously manipulated the temporal predictability and the spatial clumping of food to test whether aggression increases as food becomes more predictable in time and more clumped in space. We tested these predictions using wild Zenaida doves (*Zenaida aurita*) in Barbados because previous work showed marked differences in social behavior between two populations, apparently related to differences in the distribution of food in space and time. There was a significant interaction between the effects of the temporal predictability and spatial clumping of food. As predicted, the rate of aggression increased as the temporal predictability of food increased, but only significantly in the spatially clumped condition. Similarly, as predicted, aggression increased as the spatial clumping of food increased, but only significantly in the temporally predictable condition. In addition, the per capita rate of aggression peaked at intermediate competitor densities in the spatially clumped condition. Differences in rates of aggression observed during experimental manipulations and between the two populations during baseline observations were generally consistent with predictions of resource defense theory. *Key words*: aggression, economic defendability, feeding competition, spatial clumping, temporal predictability, *Zenaida aurita*. [*Behav Ecol* 12:490–495 (2001)]

The study of competitive aggression (sensu Archer, 1988) has traditionally been approached from two theoretical perspectives (Stamps and Krishnan, 1999). Game theory models (e.g., Maynard-Smith, 1982; Parker, 1984) predict the form and outcome of contests based primarily on asymmetries between competitors, whereas optimality models primarily predict the occurrence of territoriality based on whether the net benefits of defense are greater than the net benefits of a non-aggressive strategy; that is whether the resource is economically defendable (sensu Brown, 1964). The economic defendability of a resource is thought to depend on competitor density and at least five components of resource distribution in space and time (see Grant 1993, 1997; Warner, 1980): resource abundance (mean in an area over a particular time), spatial clumping (variance in abundance over space), temporal clumping (variance in abundance over time), spatial predictability (dependability of good sites over time, i.e., the autocorrelation of resource abundance in space over time), and temporal predictability (dependability of good times over space, i.e., the autocorrelation of resource abundance in time over space) (Davies and Houston, 1984; Emlen and Oring, 1977; Grant, 1993; Myers et al., 1981; Warner, 1980).

While territoriality has attracted much theoretical and empirical study (Stamps, 1994), it is but one form of interference competition, which also includes brief contests over a single unit of resource, the guarding of ephemeral resource patches, and dominance hierarchies (Archer, 1988). Nevertheless, resource defense theory, the loose body of hypotheses concern-

ing the occurrence of territoriality, also accurately predicts the occurrence of competitive aggression at smaller spatial and temporal scales. For instance, aggression while competing for ephemeral resources increases as those resources become more clumped in space (Grant and Guha, 1993; Monaghan and Metcalfe, 1985; Zahavi, 1971), dispersed in time (Bryant and Grant, 1995; Grant and Kramer, 1992), and predictable in space (Grand and Grant, 1994), as predicted by resource defense theory (Brown, 1964; Davies and Houston, 1984; Emlen and Oring, 1977; Grant, 1993; Myers et al., 1981; Warner, 1980). The same principles predict the strength of dominance hierarchies within groups (e.g., Isbell, 1991). Hence, the concept of economic defendability, that was originally concerned only with the occurrence of territoriality, can probably be broadened to a concept of the economic use of aggression during competition.

While many studies have demonstrated the effects of the spatial and temporal clumping of resources on the frequency of competitive aggression (see references above), few studies have investigated the effects of the predictability of resources in space and time. Dominant convict cichlids, *Cichlasoma nigrofasciatum*, became more aggressive and monopolized a greater share of the food when it was more predictable in space (Grand and Grant, 1994). However, the prediction (Warner, 1980) that aggression and monopolization of food increase as resources become more dependable in time (e.g., daily or seasonally) has not been tested.

Few studies have manipulated resource distribution in the field, while monitoring the aggressive behavior of the competitors. Notable exceptions showed that white wagtails (*Motacilla alba alba*; Zahavi, 1971) and brown hares (*Lepus europaeus*; Monaghan and Metcalfe, 1985) shifted from scramble to contest competition as their food was increasingly clumped in space (also see Davies and Hartley, 1996; Ims, 1988). Moreover, even fewer studies have manipulated more than one

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component of resource distribution at a time to test for interactions between these variables (but see Robb and Grant, 1998). In general, resource defense theory makes predictions about only one component of resource distribution at a time and assumes no interactions between components (but see Emlen and Oring, 1977). Hence, its predictions will only be applicable to the multivariate distribution of resources in the wild if the main effects of each component overwhelm any potential interactions between components.

Our study simultaneously manipulates the temporal predictability and spatial clumping of food while monitoring the aggressive behavior of a population of Zenaida doves (*Zenaida aurita*) on the island of Barbados. We chose Zenaida doves as our test species because they show striking intraspecific variation in aggressive behavior on Barbados. In most areas, doves establish year-round feeding territories that are defended against conspecifics. Territorial doves routinely use aggression to exclude conspecifics from food, but often feed nonaggressively with other avian species (*Quiscalus lugubris*, *Columbina passerina*, *Molothrus bonariensis*, and *Loxigilla noctis*) in mixed aggregations (Dolman et al., 1996; Lefebvre et al., 1996). In contrast, at the grain storage and transport facilities of the Deep Water Harbour (DWH), Zenaida doves feed in large homospecific flocks with little apparent aggression (Dolman et al., 1996). We manipulated the distribution of artificial patches of food at DWH to test the predictions that the frequency of aggression by doves will increase as both the temporal predictability and spatial clumping of food increase.

## METHODS

### Study populations

Field observations were conducted at two study areas on the island of Barbados, separated by 9 km: (1) the grounds of the Bellairs Research Institute of McGill University and adjacent Folkestone Park, both in the parish of St. James (StJ); and (2) the Barbados Feeding Mills plant in Deep Water Harbour (DWH), in the parish of St. Michael. The StJ area included a public park and beach, hotel grounds, and the Bellairs research facilities. The study area featured extensive coastal woodland of predominantly casuarina, manchineel, mahogany, and coconut trees that provide the doves with roosting, nesting, and foraging sites (Bond, 1985). The DWH is a landfill area that includes docking, grain loading, milling, and storage facilities for a wide range of animal feeds and grains (Dolman et al., 1996). This 200 × 200 m area has been cleared of most of its arboreal vegetation but frequently provides large, ephemeral patches of cereal and legume spillage as a result of storage and transport operations. Feral pigeons (*Columba livia*) are the most frequent heterospecific competitor of doves at this study area, but are normally in much smaller numbers than *Z. aurita* (Dolman et al., 1996).

At StJ, doves defend year-round territories against intruding conspecifics and forage most often alone or in monogamous pairs (Lefebvre et al., 1996). In contrast, Zenaida doves within DWH forage in large, homospecific flocks of up to 120 birds, with little apparent aggression.

### Premanipulation observations

Our study consisted of three phases: premanipulation observations at StJ and DWH, an experimental phase in which the spatial clumping and temporal predictability of food were manipulated at DWH, and postmanipulation observations at DWH.

During the first 3 weeks of January, 40 adults were caught in walk-in baited drop traps set throughout the StJ study area.

Upon capture, birds were fitted with individually colored plastic leg bands and immediately released at their point of capture. Field observations (see below) were then conducted on and around these areas of capture, using a time period and method identical to the one used at DWH (see below). Over 90% of the tagged birds were resighted during field observations. Birds were not individually tagged at DWH because two banding programs (90 individuals by Carlier and Lefebvre, 1997; 40 individuals in a pilot study for this experiment) showed low resighting rates of banded doves over the time period required for our study (31% and 15%, respectively).

Premanipulation data were collected by a single observer (JLG) on 30 days at StJ and 18 days at DWH over a 2-month period (February–March) throughout the day (i.e., 0800–1700 h) at both study areas.

Seven sites characterized by frequent spillage were selected for observations around the DWH area. Observations were made only when spills were present, otherwise no doves were present or foraging. One focal dove per session was chosen haphazardly and the following foraging information was recorded in 15-s intervals: (1) size of the foraging group to which the focal bird belonged; (2) number of paces and pecks at the ground for food; and (3) intraspecific aggression. Doves were considered part of the same foraging group if they were separated by less than 5 m (Lefebvre et al., 1996). Foraging was defined by the occurrence of at least one peck at the ground per minute. Only pecks specifically targeted towards food were counted, excluding cases in which the dove was simply searching without ingesting, pecking for grit, or using pecks at the ground in a ritualized threat display. A pace was defined as one step. Ratios of pecks per pace were calculated to estimate foraging rate at the time and place of observation. An aggressive act was defined as a chase, fight, or threat display involving the focal bird and another Zenaida dove within 5 m of the focal animal. Fights were defined as a wing slap towards or on its opponent. Threat displays were characterized by either the raising of a wing contra-lateral to the opponent or as threatening pecks, which were ritualized beak swipes at the ground in the absence of food, performed during a very characteristic parallel walk display of the two opponents.

If the focal animal withdrew from the site, was lost track of, or did not peck once within a 1-min interval (unless it was engaged in aggressive displays), observations were discontinued and a new focal individual chosen haphazardly.

### Manipulating the spatial clumping and temporal predictability of food

We manipulated the distribution of food in space and time at six sites at DWH. These sites were around and within the feeding mills plant, separated by at least 10 m from one another and 15 m from one of the seven sites used for premanipulation observations. We used a commercial mix of seed for caged birds, obtained from Tropical Fish Pets, Bridgetown, Barbados. Spatial clumping was manipulated by presenting 40 ml of seed in either an 8 × 8 cm area (clumped) or an 6 × 6 m area (dispersed). We had two levels of temporal predictability: predictable, seed was presented at the same site at 1400 h for 14 consecutive days (after 7 days of training, see below); and unpredictable, seed was presented at haphazard times each day, between 0800 and 1700 h, and on only 14 of 24 days (i.e., after 5 days of training, food was presented on days 6, 7, 9, 10, 12, 14, 15, 19, 20, 22, 25, 26, 27, and 29).

The experimental manipulations were conducted over four time periods (Table 1). Sites received the predictable treatment during periods 1 and 3 and the unpredictable treatment during periods 2 and 4, in a crossover design (Wilkinson,

**Table 1**  
**Experimental design for manipulations of spatial clumping and temporal predictability of food at six sites across four time periods**

Sites	Time Periods			
	1 (21 days) predictable	2 (29 days) unpredictable	3 (21 days) predictable	4 (29 days) unpredictable
1	T—C—D	T—D—C	T—C—D	T—C—D
2	T—C—D	T—D—C	T—D—C	T—D—C
3	T—C—D	T—C—D	T—C—D	T—C—D
4	T—D—C	T—C—D	T—D—C	T—C—D
5	T—D—C	T—D—C	T—D—C	T—D—C
6	T—D—C	T—C—D	T—C—D	T—D—C

Spatial clumping (C, clumped, D, dispersed); temporal predictability (predictable, food presented at the same time of day for 14 days consecutively; unpredictable, food presented at different times of day on only 14 of 24 days). At the beginning of each time period, the birds attending each site received a training session (T): predictable, 7 days of clumped food at the same time of day; unpredictable, 5 days of no food. After each training session, for the first half of the period three sites were randomly assigned the clumped treatment and three sites received the dispersed treatment; each site received the alternate treatment for the second half of the data collection period.

1990). Prior to periods 1 and 3, food was presented in a clumped manner at 1400 h for 7 days in a row to train the birds to expect a temporally predictable environment. Data collection began on day 8 when three sites were randomly chosen to receive the clumped treatment, and the remaining three sites received the dispersed treatment. After 7 days of data collection, each site was switched and received the alternate level of spatial clumping for another 7 days. Prior to periods 2 and 4, sites received no food for 5 days in a row to train birds that they were no longer in a temporally predictable environment. Data collection began on day 6, when three sites were randomly chosen to receive the clumped and dispersed treatments, respectively. Halfway through data collection, each site received the alternate level of spatial clumping (Table 1).

Focal animal observations were made at each site when food was present. The order of observation among sites was randomly determined; food was present at only one site at a time. The median duration of a focal observation was 45 s (range = 30–240 s). Observations of pecking, pacing and intraspecific aggression were taken in the same manner as they were in the premanipulation phase, again using 15-s intervals. In addition, any aggression with heterospecifics, chiefly shiny cowbirds (*M. bonariensis*) and Carib grackles (*Q. lugubris*) was noted, as was the number of times the focal animal was chased. The median number of focal birds observed at a site per day was four (range = 1–10). Observations at a particular site were concluded when the seeds were eaten or the birds ceased foraging. The median duration of an observation at a particular site was 5 min (range = 0.5–10 min).

#### Postmanipulation observations

Following the completion of experimental manipulations, postmanipulation data were collected at DWH every day for 7 days in the exact manner as during the premanipulation phase. We used these data to test for any seasonal changes in aggressive behavior. Our observations and experiments were conducted during the dry season (Caribbean Meteorological Institute, 1982), when reproduction is at its lowest (Wiley, 1991). However, opportunistic breeding occurred sporadically during our study.

#### Analysis

For each focal bird, the total number of aggressive acts was divided by the length of time observed (minimum 30 s) to obtain a rate of aggression. Differences among treatments at DWH were analyzed as a randomized complete block design with sites as blocks and spatial clumping and temporal predictability as the main effects. Because the same focal bird could be observed on more than 1 day, we used the average competitor density (number of doves within 5 m of the focal animal) and the average rate of aggression by focal birds at a site over the 7 days of observations as an individual datum for these analyses. When investigating the relationship between aggression and competitor density, we recorded the average rate of aggression at a particular density and site. For statistical tests, however, we used the mean rate of aggression at a particular density and treatment across all sites as an individual datum. The data met the assumptions required for parametric analyses, so transformations were not required.

We used an eight-period crossover design (Wilkinson, 1990) to test for potential carryover effects of the treatment in the previous period on the doves' behavior. We also used a repeated measures analysis of variance to test for temporal trends in behavior over the 7 days of data collected for a particular combination of temporal predictability and spatial clumping. Because neither analysis detected any significant trends, we did not present the results of these analyses; both are described by Goldberg (1998).

## RESULTS

#### Pre- and postmanipulation observations

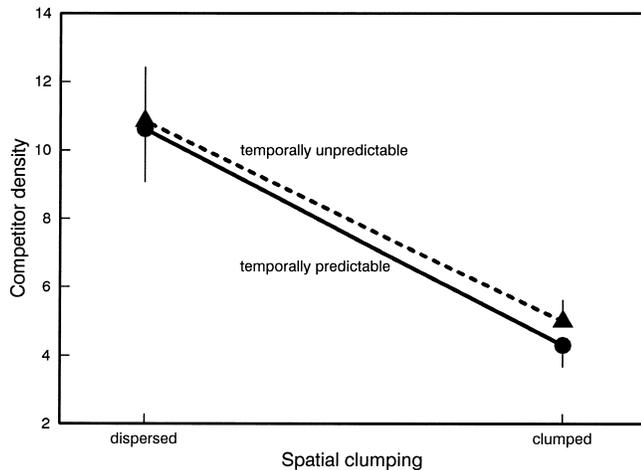
The doves at DWH routinely fed in large groups of conspecifics (median number within 5 m = 8), at high rates ( $x \pm SE$  pecks per pace =  $2.43 \pm 0.43$ ), and exhibited low rates of intraspecific aggression ( $x \pm SE$  acts/30 s =  $0.41 \pm 0.062$ ). Escalated fighting accounted for only 8% of the aggressive interactions. In contrast, doves at StJ typically fed alone (median number of conspecifics within 5 m = 0), at low rates ( $x \pm SE$  pecks per pace =  $0.019 \pm 0.002$ ), but exhibited high rates of aggression ( $x \pm SE$  acts/30 s =  $1.08 \pm 0.15$ ). Escalated fighting accounted for 20% of all aggressive interactions. The behavior observed at StJ was typical for doves observed in other parts of Barbados (Dolman et al., 1996; Lefebvre et al., 1996).

To test for seasonal differences in level of aggression, we compared the premanipulation data with those collected after the experiments were completed, 3 months later. Aggression rate did not differ between the pre- and postmanipulation observations at DWH ( $t = 1.31$ ,  $df = 241$ ,  $p = .19$ ).

#### Manipulation of spatial clumping and temporal predictability

The number of competitors within 5 m of the focal bird was significantly affected by the distribution of food. Competitor density was higher at spatially dispersed than at spatially clumped patches (Figure 1;  $F_{1,39} = 26.87$ ,  $p < .001$ ). The effects of the temporal predictability of food ( $F_{1,39} = 0.16$ ,  $p = .69$ ), the interaction between the spatial clumping and the temporal predictability of food ( $F_{1,39} = 0.04$ ,  $p = .84$ ), and site ( $F_{1,39} = 1.05$ ,  $p = .40$ ) did not significantly affect competitor density (Figure 1).

There was a significant interaction between the effects of the temporal predictability and the spatial clumping of food on the rate of aggression (Figure 2;  $F_{1,39} = 8.79$ ,  $p = .005$ ). The increase in aggression when food changed from temporally unpredictable to temporally predictable was significant in the spatially clumped condition (Tukey's HSD post hoc test,



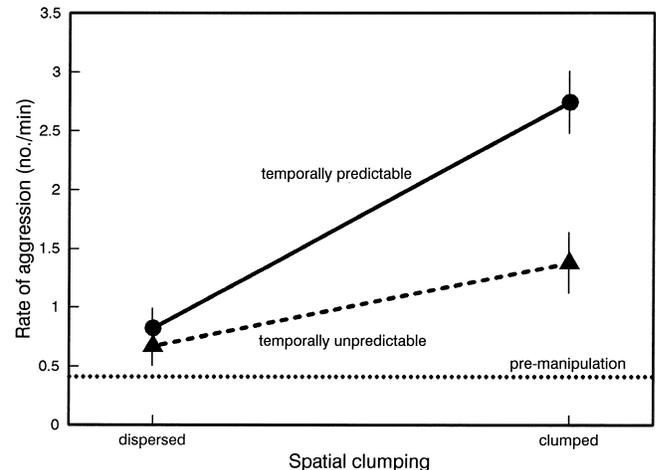
**Figure 1**  
Effect of the temporal predictability and the spatial clumping of food on the number of competitors (mean  $\pm$  SE,  $n = 12$ ) within 5 m of the focal Zenaida dove.

$p < .001$ ), but not in the spatially dispersed condition ( $p = .96$ ). Rates of aggression also tended to increase when food was spatially clumped; this increase was significant when food was temporally predictable (Tukey's HSD post hoc test,  $p < .001$ ), but not when food was temporally unpredictable ( $p = .087$ ). In spite of the significant interaction, all trends in aggression were consistent with the predictions of resource defense theory: that is, aggression increased as the spatial clumping of food increased and as the temporal predictability of food increased. Moreover, as predicted, rates of aggression were highest when food was both clumped in space and predictable in time. Rate of aggression did not differ significantly among sites ( $F_{1,39} = 2.22$ ,  $p = .072$ ).

Compared to the premanipulation data, aggression rate was significantly higher when food was either clumped in space or predictable in time (i.e., the 95% C.I. did not include the premanipulation mean). When food was both dispersed in space and unpredictable in time, the rate of aggression did not differ significantly from the premanipulation mean.

Aggression exhibited a "dome-shaped" relationship with competitor density only when food was both clumped in space and predictable in time (Figure 3a). A cubic function best described the change in aggression with competitor density ( $Y = 0.0130x^3 - 0.344x^2 + 2.318x - 0.702$ ,  $r^2 = .89$ ,  $F_{3,11} = 30.22$ ,  $p < .0001$ ); the rate of aggression initially increased with increasing competitor density, peaked at a density of about five, and then declined before increasing slightly at high densities. The cubic term explained a significant amount of the variation in rate of aggression ( $F_{1,11} = 27.19$ ,  $p = .00029$ ), even after the linear and quadratic terms were included in the model. A cubic function also described the relationship when food was clumped and unpredictable (Figure 3b;  $Y = 0.00669x^3 - 0.151x^2 + 0.847x + 0.234$ ,  $r^2 = .70$ ,  $F_{3,11} = 8.46$ ,  $p = .0034$ ). Unlike Figure 3a, however, there was a marked increase in aggression at high competitor density. In the dispersed and predictable treatment, aggression increased linearly with increasing competitor density (Figure 3c;  $r^2 = .47$ ,  $F_{1,13} = 11.58$ ,  $p = .0047$ ). However, there was no significant relationship between rate of aggression and competitor density in the dispersed and unpredictable treatments (Figure 3d).

Chasing was the primary behavior used by doves when interfering with each other at food patches (Figure 4). However, the type of behavior used differed significantly among the



**Figure 2**  
Effect of the temporal predictability and spatial clumping of food on the rate of aggression (mean  $\pm$  SE,  $n = 12$ ) directed by focal doves at conspecifics. The horizontal dotted line represents the baseline rate of aggression observed in premanipulation observations.

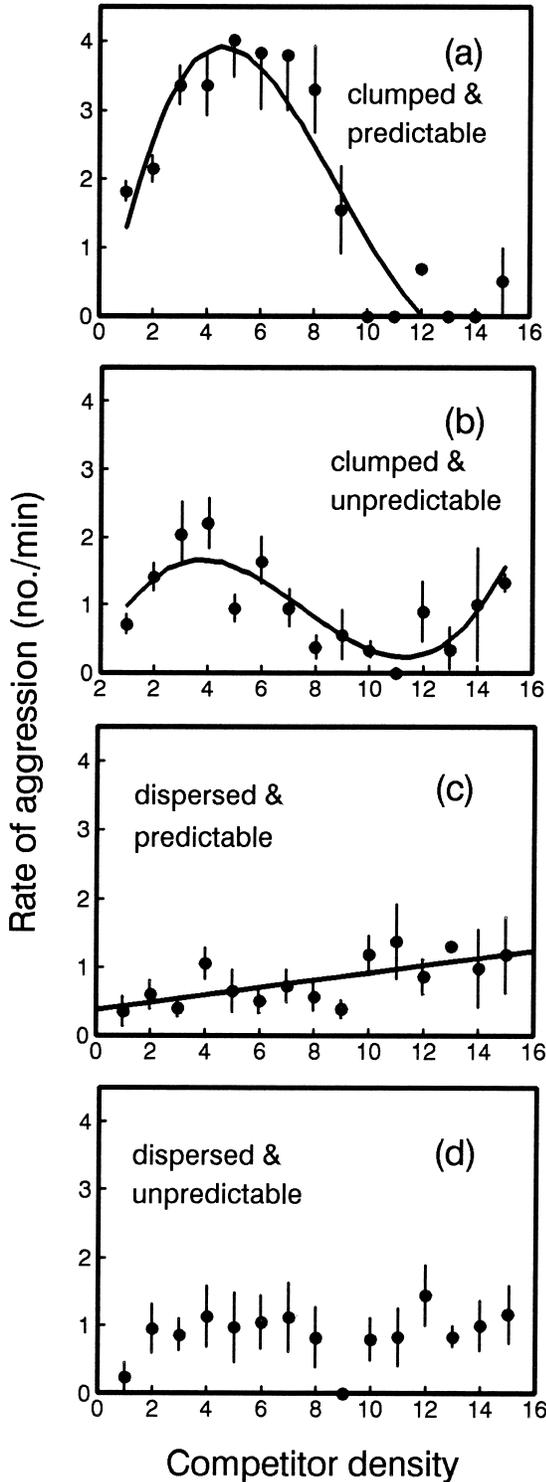
four treatments ( $\chi^2_6 = 42.0$ ,  $p < .001$ ). These differences were largely due to relatively more fights and fewer threats in the two predictable treatments than in the two unpredictable treatments ( $\chi^2_1 = 13.97$ ,  $p < .001$ ; with Yates's correction). A similar comparison between scattered versus clumped treatments revealed no significant difference in the relative use of fights versus threats ( $\chi^2_1 = 0.96$ ,  $p = .76$ ; with Yates's correction).

## DISCUSSION

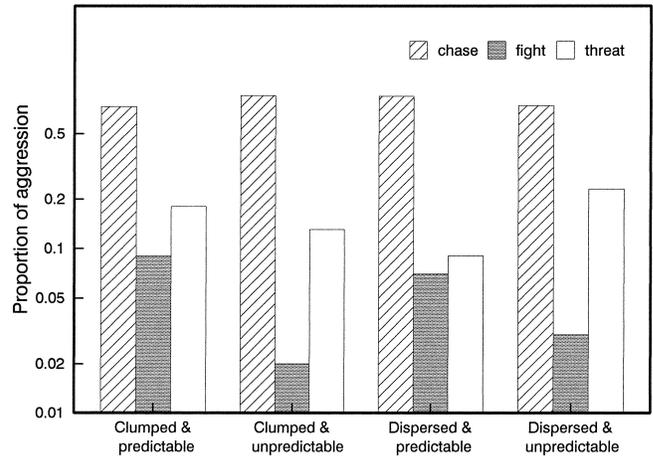
Our study provides experimental evidence that an increase in the temporal predictability of food leads to an increase in competitive aggression, at least when food was also clumped in space. The doves apparently learned that a patch was temporally predictable during the 7 days of training, as no temporal trends in behavior were apparent during data collection (see Methods; Goldberg, 1998). Two mechanisms, that are not mutually exclusive, may explain the increase in aggression at temporally predictable patches. Individual doves may become more aggressive as they learn that a patch is predictable in time, in the hope of monopolizing the patch in the future (see Grant and Kramer, 1992). Dominant convict cichlids also adjust their behavior as they became more familiar with a spatially predictable environment (Grand and Grant, 1994). Alternatively, inherently more aggressive doves may have been attracted to predictable patches, in which they were able to monopolize a large share of the food. In such a truncated phenotype ESS (sensu Milinski and Parker, 1991), less competitive doves may simply avoid clumped, predictable patches when dominants are present. Either mechanism involves learning and is consistent with the finding that doves used escalated fighting more often at predictable than unpredictable patches.

Our data also confirmed previous research showing increased aggression with an increased spatial clumping of food (Grant and Guha, 1993; Monaghan and Metcalfe, 1985; Zahavi, 1971). The lack of temporal trends in behavior following a change in the spatial clumping of a patch (see Methods section; Goldberg, 1998) suggest that doves can assess patch size with little or no learning.

Resource defense theory primarily makes verbal, qualitative



**Figure 3**  
The rate of aggression by focal doves in relation to competitor density when food is (a) clumped in space and predictable in time, (b) clumped in space and unpredictable in time, (c) dispersed in space and predictable in time, and (d) dispersed in space and unpredictable in time. For graphical purposes, the cubic function in (a) is not extended below the y-axis.



**Figure 4**  
Type of aggressive behavior used by doves in relation to the temporal predictability and the spatial clumping of food. For graphical purposes, a log scale is used for the y-axis.

predictions about how individual components of resource distribution affect the frequency of aggression or territoriality. The significant interaction between the temporal predictability and spatial clumping of food in this study and between the spatial and temporal clumping of food in Robb and Grant (1988) underline the need for quantitative, multivariate measures of resource distribution. Our study suggests that Zenaida doves will not or cannot defend an ephemeral patch of 36 m<sup>2</sup>, regardless of its predictability in time, where patches of 0.0064 m<sup>2</sup> are defendable at a variety of levels of temporal predictability. Despite the interactions, all trends in aggression, whether significant or not, were consistent with the univariate predictions from resource defense theory (also see Robb and Grant, 1998).

Competitor density was lower at smaller patches presumably because fewer doves could participate in feeding due to crowding and the effect of aggression. It was more surprising that temporal predictability had no effect on competitor density. This result suggests that the doves were highly mobile and readily joined patches discovered by others (see Giraldeau and Beauchamp, 1999), even when those patches appeared unpredictably in time.

The variation in competitor density allowed us to test the prediction that the rate of competitive aggression peaks at an intermediate competitor density (see Grant et al., 2000). In both spatially clumped treatments, aggression initially increased and peaked at a competitor density of about 4–5 doves per 5 m<sup>2</sup>. Interestingly, rate of aggression decreased at competitor densities greater than five, but then increased again at densities greater than 12. This bimodality, which is not predicted by any current theory, suggests that two processes are at work. We suspect that the high initial peak in aggression resulted from dominant doves attempting to defend and monopolize the entire patch when the number of intruders was relatively low (i.e., a short-term territory). As competitor density continued to increase, defense of the patch may have become increasingly uneconomical, so aggression decreased. The increase in aggression at extremely high competitor densities may be caused by doves becoming increasingly hawk-like (sensu Maynard-Smith 1982) in the face of increased crowding, as observed in other species of birds (Morse, 1980) and predicted by a game theory model of social foraging (Sirot, 2000). Doves made no attempt to defend the large patches in the dispersed treatment, so there was no initial peak in aggression at low densities. If anything, rate of aggression tend-

ed to increase monotonically with density, as predicted by Sirot (2000). The challenge for a unified theory of competitive aggression is to predict when animals switch from trying to defend and monopolize an entire patch to using aggression while sharing a patch with others. Patch size and competitor number are likely key variables.

Of the six key environmental variables thought to influence economic defendability (see Introduction; Grant, 1993; Warner, 1980), we manipulated temporal predictability and spatial clumping, while controlling the abundance (always 40 ml of seed per patch), spatial predictability (always the same sites), and temporal clumping (food always presented once per patch per day) of food at experimental patches. Competitor density was not controlled. The success of the manipulations at DWH was probably partly due to the uniqueness of the site; the doves were used to human activity and responding to ephemeral patches of food. Hence, they readily discovered our experimental patches and responded to the manipulations of food distribution. Similar manipulations at Stj had little effect on dove behavior (Goldberg, 1998). Virtually all patches were within a feeding territory and, hence, were discovered and eaten only by the resident pair. In addition, presumably too little food was added on too short a time scale to affect the permanent system of territories at Stj (Goldberg, 1998). The switch between defending resource patches to territories containing patches is a fundamental problem in behavioral ecology and will likely be related to the distribution of patches in space and time.

At DWH, the lower rate of aggression during baseline observations, compared to experimental conditions, was likely due to the ephemeral nature of patches resulting from anthropogenic spillage. The spilling of grain occurs unpredictably in space and time, delivering large amounts of grain in a spatially and temporally clumped manner that attracts many doves. In between spills, food was in low abundance. In contrast, during experiments food was always spatially predictable, at a moderate density, and attracted fewer doves.

Differences in behavior between the DWH and Stj populations may also be related to the distribution of food. When food was available at DWH, feeding rates were two orders of magnitude higher than at Stj (also see Dolman et al., 1996). Presumably, the high abundance of food in conjunction with the ephemeral nature of the patches and high competitor density at DWH made the defense of permanent feeding territories uneconomical. Taken together, our observations on wild Zenaida doves show that the rates of aggression were influenced by food distribution and competitor density in a manner largely consistent with the predictions of resource defense theory.

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