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Food availability, intrusion pressure and territory size: an experimental study of Anna's hummingbirds (*Calypte anna*)

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Abstract. Theoretical considerations implicate food availability and intrusion pressure as important determinants of territory size, but empirical studies have led to contradictory conclusions about cause-and-effect relationships among these three variables. To investigate this problem, we provided patches of electronically controlled artificial flowers, which were defended by male *Calypte anna*. Food availability was experimentally manipulated, and intrusion rate and territory size were calculated from behavioral observations of the territory owner. Changes in both food availability and intrusion rate were found to be significantly correlated with changes in territory size under certain conditions. Intrusion rate, which was influenced by food availability, was negatively associated with territory size so long as food availability was high. This association persisted even after possible effects of food availability were controlled statistically. Food availability was negatively correlated with territory size only when intrusion rates were high and after owners had been defending territories for 3 days. As food availability and intrusion rate increased, owners increasingly restricted their defense to the patch itself; partial regressions revealed a significant association for intrusion rate but not food availability. When intrusion rate was low and food availability varied from low to high levels, no relationship was observed between food availability and territory size, apparently because of opposing influences of food abundance on territory size.

Key words: Territory size – Intrusion – Food – Hummingbirds – *Calypte*

Introduction

Theoretical analyses predict that territory size should decrease as food availability increases under most but not all conditions (Brown and Orians 1970; Ebersole 1980; Hixon 1980; Schoener 1983). Owners may adjust territory size as a direct response to food availability, or as an indirect response through effects of food availability on intrusion pressure. Sizes of territories defended by nonbreeding sanderlings (*Chalidris alba*) are consistent with the latter possibility (Myers et al. 1979a). Territory size was negatively correlated with both food density and intruder pressure. After accounting for the association between food density and intrusion pressure statistically, territory size was still associated with intruder pressure but not food density (Myers et al. 1979a). Because this study accounted for food abundance statistically rather than experimentally, it did not prove that food abundance has only indirect effects on territory size. A significant partial correlation between intrusion pressure and territory size also could have occurred if prey density directly influenced territory size, and intruders used the density of territories (or territory owners) as an indicator of food availability. Areas of high owner density might also be attractive to intruders because the risk of predation is lower (Hamilton 1971), or because such areas allow intruders to efficiently assess, and perhaps challenge, territory owners.

This plausibility of alternative explanations draws attention to the need for experimental manipulations of food abundance and intrusion rate. In the reef fishes *Parma victoriae* and *Chaetodon multicinctus*, territory size decreased in response to experimental increases in competitor abundance but not to changes in food availability (Norman and Jones 1984; Tricas 1989).

Studies of nectarivorous birds have yielded seemingly inconsistent relationships among territory size, food availability, and intrusion rate. In rufous hummingbirds (*Selasphorus rufus*), reductions in natural flower densities led to an increase in territory size (Hixon et al. 1983). Intrusion pressure was not measured; however, time spent in territorial defense did not change following changes in flower densities. These experimental studies accord with nonmanipulative studies of nectarivorous birds, which document strong negative correlations be-

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tween food abundance and territory size (Gass et al. 1976; Gill and Wolf 1975; Kodric-Brown and Brown 1978). Although the potential importance of intrusion pressure in these systems has been suggested (Gass 1979), these nonmanipulative studies did not quantify intrusion pressure. In black-chinned hummingbirds (*Archilochus alexandri*), territory size decreased when intrusion pressure was experimentally increased and food on territories was provisioned at a constant rate (Norton et al. 1982). A correlative study of New Holland honeyeaters (*Phylidonyris novaehollandae*), however, did not find an association between intrusion pressure and territory size (McFarland 1986). In contrast to the trend found among sanderlings, food abundance was negatively correlated with territory size when intrusion pressure was controlled statistically, but intrusion pressure was not significantly correlated with territory size when food abundance was controlled statistically (McFarland 1986). Thus, in contrast to studies of sanderlings and the other kinds of organisms mentioned above, studies of nectarivorous birds have tended to emphasize the direct influence of food abundance on territory size rather than its indirect influence through the intervening variable of intrusion pressure.

This emphasis is consistent with experiments in which food abundance influenced intrusion rate weakly if at all (Ewald and Carpenter 1978; Ewald and Bransfield 1987). The more recent confirmation of a strong effect of food availability on intrusion rate (Marchesseault and Ewald 1991), however, draws attention to the need to evaluate experimentally whether food availability influences territory size of nectarivorous birds through its effects on intrusion rate. This need is highlighted by a study of harriers (*Circus cyaneus*), which showed that changing environmental conditions change the relative importance of food abundance and intrusion pressure in explaining the size of feeding territories (Temeles 1987).

With these uncertainties in mind we investigated regulation of territory size by Anna's hummingbirds (*Calypte anna*) using experimental manipulations of food provisioned from patches of artificial flowers. We sought to determine whether changes in territory size were direct responses to manipulations of food abundance, or responses to changes in intrusion rate caused by these manipulations.

We also considered resource patchiness. Models of territory size typically assume that spatial distributions of resources are uniform (Dill 1979; Ebersole 1980; Hixon 1980; Schoener 1983). In nature, however, resources are often distributed in patches (Stiles 1973). By defending a "buffer area" around food patches, owners may intercept intruders before they can reach the patch, thereby reducing theft of food. This interception should be especially profitable for owners of rich patches because even a short intrusion on a rich patch may result in substantial loss of food. Owners of poor patches, on the other hand, could deplete the resources on their territories by their own feeding activity, thereby decreasing both intrusion success (see Charnov et al. 1976; Ewald and Orians 1983; Paton and Carpenter 1984), and the benefits of defending a large buffer area.

The preceding arguments apply when intrusion rate is sufficiently low that intrusions occur singly. As intrusion rate increases, the net gain from defense of such buffer areas should decrease, because while an owner is preoccupied in the longer chases away from the flower patch, additional intruders would be better able to feed on the territories. Thus, when intrusion pressure is low and food is patchily distributed, territory size might be positively correlated with food availability on the territory. If intrusion pressure increases uniformly as food availability on the territory increases, owners of extremely rich territories might have to defend small buffer areas because of high defense costs, yielding a negative correlation between food abundance and territory size.

Although *C. anna* defend extensive buffer areas during the breeding season, the existence and significance of buffer areas during the nonbreeding season has not been empirically investigated (Pitelka 1951; Stiles 1973). Buffer defense in nature could be masked by a gradual diminution of flower density around core patches. In such situations it would be difficult to determine whether peripheral areas (considered "edge" areas by Paton and Carpenter 1984) are defended at least partly because they act as a buffer against theft of food from the central areas.

Methods

Species and study site. Anna's hummingbirds are ideal subjects for the study of territorial behavior for several reasons. Because of their high metabolism, short-term variations in their intake and expenditure of energy can have important effects on their survival and reproduction. Moreover, they readily defend both natural and artificial nectar sources, respond quickly to changes in nectar resources, and may be easily observed (Ewald and Carpenter 1978).

The study was conducted during July and August 1989 at the Hastings Natural History Reservation, located in the foothills of California's Santa Lucia mountains and operated by the University of California, Berkeley. A population of about 100 birds was attracted to the study site by setting out about 30 feeders approximately 1 month prior to the study. Each feeder provided 20% (w/w) sucrose solution at an unrestricted rate. Very few natural flowers [*Epilobium* (= *Zauschneria*) *californica*] were present during our study, which took place during a drought year. The hummingbirds were therefore almost entirely dependent on our artificial flowers for nectar-type food.

Anna's hummingbirds (*Calypte anna*) were more common than the other hummingbird species present at the site (*Archilochus alexandri*, and occasional *Selasphorus sasin* and *S. rufus*), and also were most successful in establishing territories, presumably because they are larger (Stiles 1973; Ewald and Rohwer 1980). All the observed territorial behavior was associated with feeding rather than breeding territories, so agonistic interactions resulted from the need to acquire sufficient energy for survival.

Experimental procedure. Each patch of 20 electrical flowers was provided as a food source to be defended by a territorial individual. Our artificial flower was a modified version of "Rosey's sugarwort" (plans for the archetype were provided by M. Rosenzweig); it consisted of microbore tubing that transported nectar from a reservoir through a solenoid (which pinched the tubing) to a red-tipped corolla. The solenoid was timed to open at intervals by an electrical circuit, which was powered by a battery charged by a solar panel. The reservoir was filled with 20% sucrose solution (w/w), which flowed from the reservoir to the corolla when the solenoid was open. All flowers in a given patch were connected to the same electrical circuit.

Each replicate included an experimental and a control patch of artificial flowers. The distance between the two patches was great enough to ensure that both would not be defended by the same individual. Each patch was placed in a defendable location, i.e., next to trees and shrubs that would provide an owner with both sunny perches and shady perches from which the patch could be defended. A third patch that supplied large amounts of food was placed in the center of the field, and was continually available throughout the study. Its placement far away from shady perches made it undefendable, but provided the population of hummingbirds with a foraging alternative to intruding on defended patches.

The 20 flowers in each patch were spaced 1.5 m apart in a grid with four rows and five columns, with each flower being a cartesian coordinate integer. Locations for behaviors which occurred off the grid were estimated to the nearest tenth of an inter-flower interval, and the vertical component of a location was estimated to the nearest 0.1 m above the level of the flowers. At daybreak on day 1 of each replicate, the experimental and control patches were made available, set to provide food at the same rate. At these premanipulation settings, a patch provided about 2–3 times an owner's daily energy requirements at a constant rate; feedings by owners and intruders tended to empty the flowers throughout the day. At daybreak on day 3, the productivity of the experimental patch was reduced.

At some point during days 1 and 3, each territory was observed briefly so that the owner could be recognized upon his arrival the following morning. Owners and intruders were identified by distinctive plumage patterns and marking dye. The dye was applied to the birds using dye-coated perches, which were attached to some feeders. By sitting on the perches, birds acquired dye on their feet and abdomens; subsequent preening distributed the dye through their feathers in unique patterns. Binoculars were used when necessary to aid in the identification of individuals. Continuous dawn-to-dusk observations on days 2 and 4 were made by pairs of observers: one member of the pair observed the activities on the territory and communicated this information to the other, who recorded the data using a laptop computer. Occasionally, when activity levels were especially high, an additional observer reported to the recorder.

Upon completion of each replicate, the patch was moved, and the owner was provided with two unlimited point-source feeders. This procedure maintained independence of data points by preventing the owner from taking over new territories later in the study.

Territory size and intrusion rate calculations. We used mean chase radius as an indicator of territory size. The radius for a given chase was defined as the distance from the location of the chased bird at the initiation of the chase (termed "chase location") to the center of the territory. This center was defined as the weighted mean of all chase locations recorded during the day. A chase radius from this center was computed for every chase location. All of the chase radii for a given day were then averaged to yield a mean chase radius.

We used mean chase radius rather than estimates of territory area for several reasons. Measures of territory area (such as minimum convex polygons) are generally inflated by increased sample size, and the total number of chases per value of territory size varied by more than an order of magnitude, from less than 50 to more than 500. Second, our territories consisted of food patches surrounded by vast areas devoid of nectar. Because the nectarless areas were undefended by competing hummingbirds, owners were free to occasionally chase an intruder at great distances from the central patch, even though most intruders remained unchased at these distances. Although we observed these long chases to be rare relative to the chases on or near the patch, their presence is indicative of an occasional tendency to defend a large area. Although this tendency should be included in indicators of territory size, calculating the area based on the perimeter defined by these chases would ignore the information inherent in the vast majority of chases that occurred in the more exclusive areas within or near the patch. Mean chase radius, in contrast, subsumes the information inherent in chases at all locations and weights them according to their frequency. These considerations can be understood in terms of territory boundaries. Calculations of territory area are most informative when territory boundaries are distinct. In our system, however, territory boundaries were indistinct because tendencies to evict intruders diminished gradually as a function of distance from the central patch. We therefore believe that mean chase radii are more accurate indicators of tendencies to spatially expand or contract territories than are the areas enclosed by the most distant chases. Our decision to use mean chase radius as an indicator of territory size was made prior to any analyses of the data; we did not calculate any other measure of territory size during our analyses.

To quantify intrusion pressure we calculated the number of intrusions per territory per hour. In theory, we defined intrusions to be any entrance within the perimeter of the defended area. In practice, however, we did not know the perimeter of the defended area while we were recording data. We therefore recorded any locations of incoming birds that might reasonably be defended during our observation period. Locations in this sense refer to the points at which the birds perched, hovered, or abruptly changed direction. Upon proof-reading the data files prior to computer-read data reduction, we then entered these observations in the proper format for intrusions if they were within the chase perimeter. A small proportion of the birds were clearly flying past the territory rather than flying to it. Owners occasionally chattered at these birds, but generally seemed to ignore them. Because these birds did not slow down, we could not assign a location for them. Generally they passed above or to the side of the three-dimensional defended area. Because territories were centered around isolated patches most birds flying in questionable areas were moving toward the territory. If we missed a bird in the outskirts of the territory we were therefore likely to see it when it moved closer. Our quantification of intrusion rate was therefore probably not as error-prone as might be the case in other kinds of territorial systems with other food distributions. Because most of the birds that we missed in these peripheral areas were probably not flying toward the territory, their omission from the analysis is consistent with our measure of intrusion pressure close to the territory, which excluded birds that were flying through the territory without slowing down (see above).

Number of intrusions (rather than duration of intrusions) was used for two reasons: we wanted a measure of competitor pressure which would not be affected by the owner's response to intrusion, and we were not attempting to quantify actual energy losses to intruders. The number of intrusions included the intruders chased away by the owner, as well as intruders visiting the patch while the owner was away, and intruders which were seen by the observers to be on the territory or in areas from which other intruders had previously been chased. The average intrusion rate for each day was used in all calculations.

Intrusion pressure was calculated per territory rather than per unit area because our observations indicated that virtually all chased intruders were coming toward the territory. Changes in territory size therefore would not alter appreciably the frequency of encountered intruders.

Intrusion rate and productivities were $\log_{10}$-transformed to normalize variances. A $\log_{10}(p+1)$ transformation was used for nectar provisioning rates (p) because the productivity of one experimental patch was reduced to zero. A $\log_{10}(10i)$ transformation was used for intrusion rate (i).

Data base. We completed 11 replicates during the study season. All but one of the observation sessions involved territories defended by male *Calypte anna*. The only exception occurred when a juvenile *Selasphorus* (*S. sasin* or *S. rufus*) defended an experimental patch during the postmanipulation day of observation. Since this study is concerned with the territorial behavior of Anna's hummingbirds, data pertaining to the *Selasphorus* territory were excluded from our analysis.

As a result of an electrical failure during the premanipulation period in one replicate, the productivity of one control territory was about 25% lower during the premanipulation day of observation than during the post-manipulation day of observation.

To reduce error due to small sample sizes we required a minimum of five observations (i.e., chase locations or intrusions) whenever ratios were calculated. Statistical tests were two-tailed unless noted otherwise.

Results

Territory radius

On pre-manipulation territories, territory radius was significantly negatively associated with intrusion rate [Fig. 1a, $P<0.001$, r(=regression coefficient)$=-0.69$, $n=22$], but not with productivity (Fig. 2a, $P=0.09$, $r=-0.37$, $n=22$), which was experimentally maintained over a relatively narrow range. When the effects of productivity were accounted for statistically, intrusion rate was still significantly negatively associated with territory radius [$P<0.001$, r_p(=standardized partial regression coefficient)$=-0.64$, $n=22$]. When intrusion rate was controlled statistically, however, productivity was not significantly associated with changes in territory radius ($P=0.28$, $r_p=-0.19$, $n=22$).

During the post-manipulation period, in which a wider range of productivities was represented, territory radius was not significantly associated with either intrusion rate (Fig. 1b; $P=0.37$, $r=-0.20$, $n=21$) or productivity (Fig. 2b: $P=0.76$, $r=-0.07$, $n=21$). Partial regressions were not significant for territory radius as a function of either intrusion rate ($P=0.21$, $r_p=-0.59$) or productivity ($P=0.34$, $r_p=+0.44$).

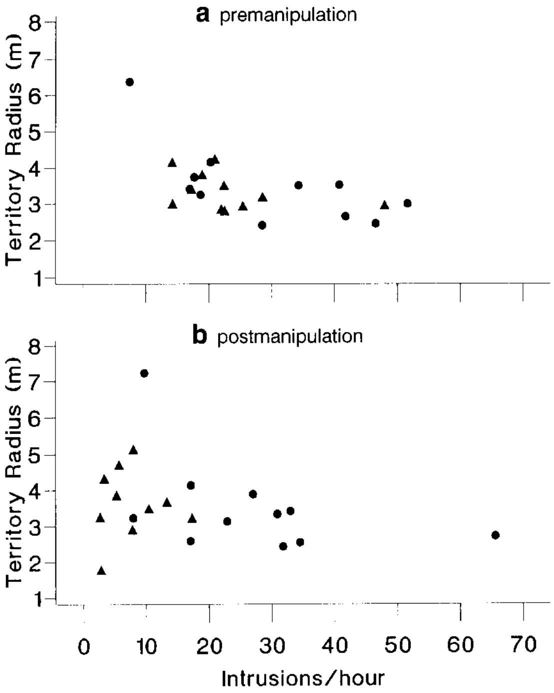

Fig. 1a, b. Mean territory radii as a function of intrusion rate per territory. ▲ Experimental territories; ● control territories. Each *data point* subsumes chases on the grid and in the buffer for a given territory. **a** Territories prior to experimental reductions of patch productivity; **b** territories after experimental reductions of patch productivity

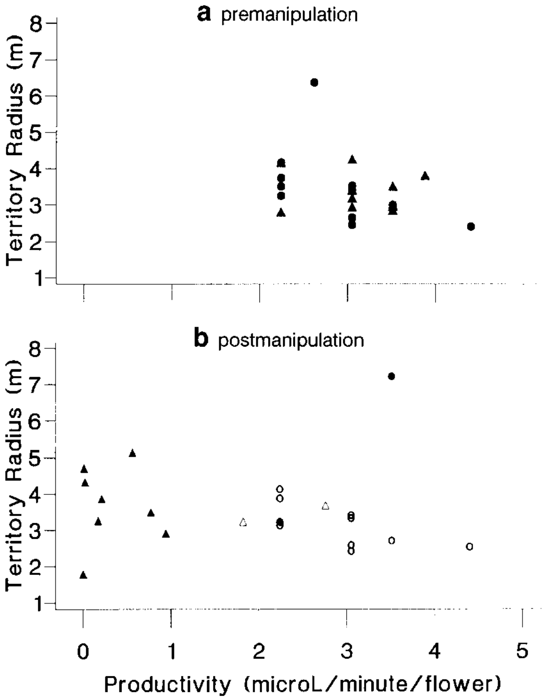

Fig. 2a, b. Mean territory radii as a function of productivity. **a** Territories prior to experimental reductions of patch productivity; symbols as in Fig. 1. **b** Territories after experimental reductions of patch productivity; △ experimental territories, high intrusion; ▲ experimental territories, low intrusion; ○ control territories, high intrusion; ● control territories, low intrusion

The lack of associations between these variables could be a consequence of opposing effects of food abundance on territory radius. When intrusion pressure on a resource patch is low, owners may defend larger rather than smaller territories as food abundance increases (see Introduction). When intrusion pressure is moderate to high, however, increased food abundance apparently leads to decreased territory radius by increasing intrusion pressure (see Figs. 1a and 2a, and Marchesseault and Ewald 1991).

To investigate such opposing effects we separated those postmanipulation territories with the ten lowest intrusion rates, which we termed "low-intrusion" territories, from the remaining "high-intrusion" territories. Our use of the ten lowest rates balanced the need for very low intrusion rates against the need for a statistically meaningful sample size.

The relationship between productivity and territory radius depended on intrusion rate. On high-intrusion territories, chase radius was significantly negatively associated with productivity (open symbols in Fig. 2b, $P<0.05$, $r=-0.62$, $n=11$), but not with intrusion rate ($P=0.17$, $r=-0.45$, $n=11$). In contrast, on low-intrusion-rate territories territory radius was not significantly associated with productivity, though there was a trend toward a positive association (closed symbols in Fig. 2b,

$P = 0.16$, $r = 0.48$, $n = 10$); the slope of this positive trend between territory radius and productivity was significantly different from the slope of the corresponding negative regression on high-intrusion territories (one-tailed $P < 0.05$, $n = 21$). These results suggest that when intrusion rate is low, the compressive effect of intrusion rate on territory size is offset by a tendency for owners to expand their territories in response to increased food availability.

The preceding results show that productivity, but not intrusion rate, is negatively and significantly associated with territory radius on high-intrusion-rate, postmanipulation territories. One could argue that this result was a statistical consequence of the reduced variation in intrusion rate that occurred when the analysis was restricted to territories with high intrusion rates.

To evaluate this possibility, we quantified the independent effects of intrusion rate and productivity on territory radius by calculating partial regression coefficients for the high-intrusion-rate data. Neither coefficient was statistically significant, probably owing to the strong dependence of intrusion rate on productivity (Marchesseault and Ewald 1991; the variation that is accounted for by this dependence is excluded by the partial regression analysis, even though it contributes to the significant correlation represented by the open symbols in Fig. 2b). The magnitude of the partial regression coefficient describing the effect of productivity on territory radius, however, was more than 3 times the coefficient describing the effect of intrusion rate (for effects of productivity, $r_p = -0.49$, $P = 0.08$; for effects of intrusion rate $r_p = -0.14$, $P = 0.35$; $n = 11$, one-tailed tests). Taken together, the simple and partial regressions indicate that when intrusion rates are high, there is an effect of productivity on territory radius that is independent of any effect through the intervening variable of intrusion rate.

To assess whether the significant association between intrusion rate and territory size documented in the premanipulation data was present in the postmanipulation data, we compared the results from control territories. This allowed us to see if, on territories consistently providing high (control) amounts of food, the associations between intrusion rate, food availability and territory size changed over time. Within each data set, territory radius was significantly related to intrusion rate (premanipulation: $P < 0.005$, $r = -0.81$, $n = 11$; postmanipulation: $P < 0.05$, $r = -0.54$, $n = 11$; one-tailed tests) but not to productivity (premanipulation: $P = 0.15$, $r = -0.46$; postmanipulation: $P = 0.96$, $r = -0.02$). Partial regressions also showed that territory radius on controls was significantly related to intrusion rate (premanipulation: $P < 0.005$, $r_p = -0.74$, $n = 11$; postmanipulation: $P < 0.05$, $r_p = -0.63$, $n = 10$; one-tailed tests) but not to productivity (premanipulation: $P = 0.48$, $r_p = -0.16$; postmanipulation: $P = 0.48$, $r_p = +0.23$). The negative relationship between territory radius and intrusion rate found among the premanipulation data, therefore, was present to a lesser extent among the postmanipulation data, so long as comparable ranges of productivity are analyzed.

These partial regressions among control territories suggest that productivity does not have a significant negative effect on chase radii during either pre- or postmanipulation periods. Yet, among postmanipulation territories experiencing high intrusion rate, the partial correlations indicate that productivity did have a negative effect on territory size (open symbols in Fig. 2b). To determine whether productivity might similarly influence the radii of premanipulation territories, we restricted the analysis to the range of intrusion rates found among the postmanipulation "high-intrusion" territories; all but one territory fell within this range. The resulting negative relationship between territory radius and productivity was near the borderline of statistical significance ($P = 0.06$, $r = -0.42$, $n = 21$). Partial regressions, however, were statistically significant and negative for intrusion rate ($P < 0.05$, $r_p = -0.42$) but not for productivity ($P = 0.13$, $r_p = -0.31$). The range of productivity used in this premanipulation test did not extend as low as that used in the postmanipulation test; restricting the postmanipulation test to the same range, however, still shows a statistically significant association between postmanipulation territory radius and productivity (for the simple regression, $P = 0.02$, $r = -0.71$, $n = 10$; for the partial regression, $P < 0.05$, $r_p = -0.65$, one-tailed test).

The preceding data can be summarized as follows. Intrusion rate was negatively associated with territory size at high productivities during both premanipulation and postmanipulation periods. Productivity may have negatively influenced territory size independently of intrusion rate when intrusion rates were high during the postmanipulation period.

Defense of buffer areas

The previous analyses took into account all chases made by the owner, regardless of location. To assess whether the changes in territory radius involved a tendency to restrict defense to the flower patch, we separated chases against intruders on the patch from those that occurred in the buffer area surrounding the patch.

Territory owners shifted their defense from buffer areas to patches as intrusion rate increased. This shift occurred in both premanipulation and postmanipulation data (Fig. 3, $P < 0.005$, $r = 0.61$, $n = 20$ and $P = 0.0001$, $r = 0.79$, $n = 22$, respectively). An analogous but weaker shift was associated with higher productivities. This trend was statistically significant only after the experimental manipulation, which yielded a wider range of productivities (Fig. 4; premanipulation: $P = 0.09$, $r = 0.37$, $n = 22$; postmanipulation: $P < 0.01$, $r = 0.62$, $n = 20$).

When the effects of productivity are controlled statistically, higher intrusion rates were still significantly associated with reduced buffer defense (premanipulation: $P < 0.01$, $n = 22$, $r_p = -0.54$; postmanipulation: $P < 0.005$, $n = 20$, $r_p = -0.92$). But when intrusion rate was controlled statistically, productivity was not significantly associated with changes in buffer defense (premanipulation: $P = 0.25$, $n = 22$, $r_p = -0.22$; postmanipulation: $P = 0.60$, $n = 20$, $r_p = +0.15$).

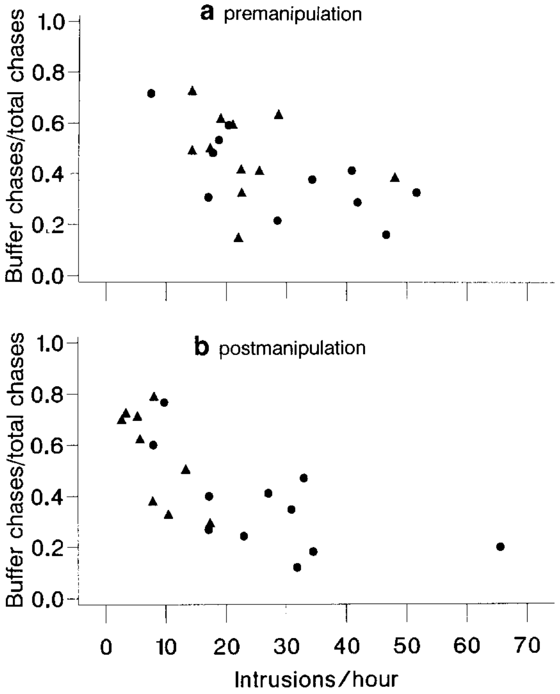

Fig. 3a, b. Proportion of chases in buffer area around patch as a function of intrusion rate; **a** premanipulation; **b** postmanipulation. Symbols are as in Fig. 1

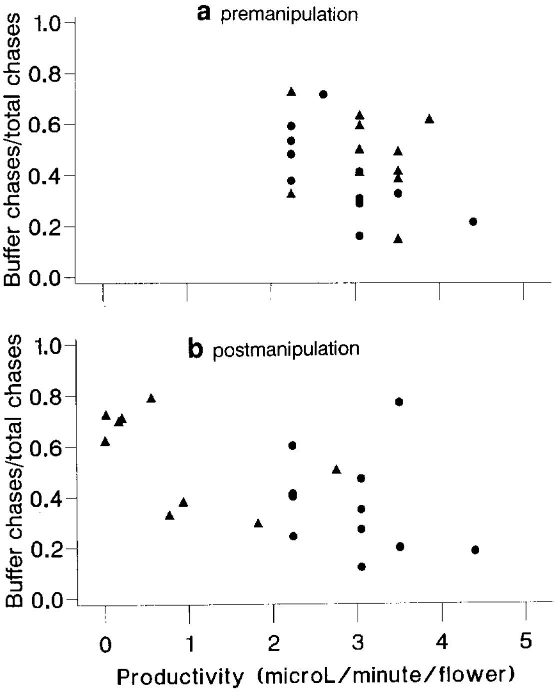

Fig. 4a, b. Proportion of chases in buffer area around patch as a function of productivity; **a** premanipulation; **b** postmanipulation. Symbols are as in Fig. 1

The negative association of intrusion rate and territory radius was not present when the analysis was restricted to chases of intruders who had entered the patch ($P > 0.2$ for each of the analogous comparisons). Overall, the average grid chase radius was 2.46 m (± 0.26 SD), which is nearly the same as the average distance of all flowers in the patch from the grid's geometric center (2.48 m). The reduction in territory size with increasing intrusion rates is therefore attributable to reductions in the defense of areas around, instead of within, the food patch.

When patch productivity and intrusion rate were low on postmanipulation territories, chase radii were not relatively long (Fig. 1b). Yet, owners tended to initiate chases in the buffer area whenever intrusion rate was low, even when patch productivity was low (Figs. 3b and 4b). These findings indicate that when productivity was low, the increased buffer defense did not extend far beyond the patch boundary.

Discussion

The results of this study reveal a more complex relationship between food availability, intrusion rate and territory size than those revealed by most previous empirical studies. During the 2nd day after territory establishment on rich patches, variation in territory size is best explained by variation in intrusion rate. After the range of territory productivity was experimentally broadened to include very poor as well as rich territories, neither productivity nor intrusion rate explained a significant amount of the variation in territory size across the entire range of intrusion rates and productivities. But when intrusion rates were high, productivity was negatively associated with territory size whereas intrusion rate was not. When intrusion rates were low this negative association vanished. Conversely, when productivity was high, intrusion rates explained a significant amount of variation in territory size whereas productivity did not.

Our findings accord with predictions that productivity can have both positive and negative effects on territory size. Theoretically, the positive effects should be most apparent when resources are patchy and costs of expansion into buffer areas are low. Accordingly, postmanipulation data show that the familiar negative relationship between territory productivity and territory size is present at high intrusion rates but absent at low intrusion rates. When intrusion rate is low increased productivity increases the energy available for defense, but it also probably increases the value of defending buffer areas around food patches because owners are less able to depress food abundance by their own feeding. Low intrusion rates may thus contribute to expansion of territories into buffer areas around rich territories, offsetting the negative relationship between productivity and territory size that would otherwise occur.

In this study, changes in territory size involved primarily extensions and contractions of defense in the buffer area. Our findings emphasize that both theoretical and empirical studies need to consider the value that peripheral areas confer by acting as a buffer to more central areas in addition to the value of the food present in these peripheral areas (cf. Paton and Carpenter 1984).

Although territory radius was not negatively associated with productivity over the entire range of postmanipulation productivities, the ratio of buffer chases to patch chases was. When intrusion rate was low, owners still chased more frequently in the buffer area, even when productivity was low. The difference between these radius and ratio data indicates that owners of low productivity territories chased a relatively short distance into the buffer area. The ratio of buffer chases to patch chases was negatively associated with intrusion rate. This finding supports the idea that increased defense costs cause a shift from buffer defense to patch defense.

Our results indicate that the direct effect of productivity on territory size becomes stronger as owners become established on territories with high intrusion rates and stable, rich food supplies. As owners become established, they may adjust their territory size more to productivity and less to intrusion rate for several related reasons. First, owners may develop a better estimate of the overall quality of their territory and may therefore become more able to adjust territory size directly to food abundance. Second, because intruders learn to distinguish rich from poor territories, a greater amount of the variation in intrusion pressure will be explainable by food abundance, and will therefore be eliminated from consideration of partial regressions of territory size on intrusion rate. Third, the net insurance benefit of defending excess food should decline as owners assess their territories to be both rich and stable. Erratic food abundance on a territory is an indication that owners may benefit from defending more food than they need as an insurance policy against periods of food shortage (Ewald and Carpenter 1978). Under such uncertain conditions, owners may respond more to the costs of defense (i.e., to intrusion rate) than the current benefits (i.e., productivity) (Myers et al. 1979b; Lima 1984). Stable, rich food supplies, in contrast, indicate higher future reliability. When reliability is high, the benefits of an insurance policy are low. Owners experiencing stable, rich territories with high intrusion rates for longer amounts of time therefore should benefit by relying more heavily on food abundance as a cue for adjusting territory size; they do not pay the insurance premiums (defense costs) for insurance benefits that they are less likely to need (see also McNair 1987).

Whatever the exact mechanism, the associations between territory size, productivity, intrusion rate, and duration of ownership reported here offer a resolution to seemingly contradictory data in the literature. On the basis of data from sanderlings, Myers et al. (1979a) concluded that intrusion pressure directly affected territory size and productivity did not. On the basis of data from honeyeaters, McFarland (1986) made the opposite conclusion. Honeyeater food sources and feeding territories are apparently more abundant and stable than those of the sanderlings (Carpenter 1978; McFarland 1986; Armstrong 1991). The sanderling system therefore seems to exhibit the two factors that our study links with weak negative effects of food abundance on territory size – temporally unstable territories and the presence of some low-quality, low-intrusion-rate territories. Like Myers et al. (1979a) we found a nonsignificant positive partial regression coefficient for productivity and territory size when these two factors were present (i.e., our postmanipulation data taken in its entirety) and significant negative associations between territory size and intrusion pressure. Like McFarland (1986), however, we found a significant negative effect of productivity on territory size under more stable circumstances (in our system, this relationship was true only for high-intrusion territories).

Our conclusions about the effects of intrusion rate and food availability on territory size are particularly congruous with data from harriers across a spectrum of environmental conditions (Temeles 1987). Territory sizes were more strongly dependent on food abundance during a year in which the density of their rodent prey was high and stable than during a year when rodent density was often low.

Our results are also consistent with experimental manipulations of territory size in other species of hummingbirds. Increases in intrusion rate decreased the sizes of feeding territories defended by black-chinned hummingbirds (Norton et al. 1982) and reductions in food abundance increased territories defended by rufous hummingbirds (Hixon et al. 1983). The expansions of territories defended by rufous hummingbirds occurred in an area where food abundance had been high for many days prior to the manipulation, where territory owners remained resident for about a week, and where owners expanded into undefended, adjacent areas (Hixon et al. 1983; Carpenter et al. 1983). These conditions are similar to the conditions under which we found a significant association between food availability and territory size.

Because the richness of flowers is more readily assessable than the richness of invertebrates hidden in the sand, the visual inspection of flowers coupled with sampling of quality over a matter of days is apparently sufficient to permit hummingbirds to adjust their territory size directly to food productivity. If stable, rich food supplies have the influence proposed above, sanderlings and other animals defending difficult-to-assess food supplies, should, like the harriers and Anna's hummingbirds, show stronger direct effects of food on territory size in habitats where the food is rich and stable over time.

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