

successful, however, and I believe that successful rapes ending in sperm transfer are rare. I never found semen deposition on the Cliff Swallow model, although similar studies by other investigators have found semen near the cloacal region of model Bank Swallows (Hoogland and Sherman 1976) and Savannah Sparrows (*Passerculus sandwichensis*) (Weatherhead and Robertson 1980).

Females might increase or decrease their fitness by participating in extra-pair copulations with males of unknown fitness. Presumably, it is to the female's advantage to copulate conservatively with males of known fitness (i.e. their mates) and not to risk decreased fitness by mating with other males.

J. P. Goossen assisted in the field, J. P. Savard and G. E. J. Smith provided statistical advice, R. J. Cannings from the Vertebrate Museum at the University of British Columbia supplied some Cliff Swallow models, and M. D. Beecher, D. R. Flook, K. Vermeer, and P. Weatherhead commented on the manuscript. I thank all of you.

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**Effect of Intrusion Pressure on Territory Size in Black-chinned Hummingbirds**  
(*Archilochus alexandri*)

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Within many avian species, territory size is inversely correlated with food abundance (Pitelka et al. 1955, Gass et al., 1976, Myers et al. 1979). Two hypotheses have been proposed to explain these correlations: (1) animals may assess resource availability directly and defend areas that contain sufficient amounts of food, or (2) animals may adjust territory size in response to an intermediate variable, intrusion pressure. By the second hypothesis, areas of greater food abundance are more costly to defend because they attract more competitors, the result being smaller territories.

Myers et al. (1979) tested these hypotheses in studies of wintering Sanderlings (*Calidris alba*). Their results supported the second hypothesis: when the interaction of prey density and intrusion pressure was controlled statistically, the effect of food density on territory size was no longer significant, yet the correlation between intrusion pressure and territory size was highly significant. Furthermore, when intrusion pressure declined seasonally while prey densities re-

mained constant or increased, territory size doubled. This increase in territory size was attributed to the decreased intrusion pressure. Similarly, Ewald et al. (1980) documented an inverse correlation between intrusion pressure and territory size in a colony of Western Gulls (*Larus occidentalis*). Because gulls do not forage on their territories, variations in food abundance could not have caused the variation in territory size in this colony.

These two hypotheses, however, need not be mutually exclusive. Hixon (1980) developed a model of optimal territory size in which he dealt with both food availability and intruder density. Integral to his model is the assumption that these two factors can vary independently of each other, but he points out that disproportionately high food production in a given territory in comparison with surrounding territories might cause a concurrent increase in intrusion pressure. Thus, theoretically, these two factors can act together and have the same effect on territory size.

Ewald et al. (1980), Myers et al. (1979) and Hixon (1980) all suggest that further studies are needed on species in which intrusion pressure and food abun-

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dance can be experimentally manipulated. In the present study, we investigated the effect of intrusion pressure on the sizes of territories defended by nonbreeding Black-chinned Hummingbirds (*Archilochus alexandri*). Specifically, we provisioned food at a constant rate while experimentally manipulating intrusion pressure. Because the rate at which food was supplied was held constant, this experiment tested whether or not increased intrusion pressure would cause a decrease in territory size. We emphasize that the null hypothesis of this test is that territory size is not inversely correlated with intrusion pressure. Rejection of this null hypothesis is not a rejection of the hypothesis that food abundance influences territory size directly.

We gathered data to test our prediction between 2 and 19 August 1980 at the Starr Ranch Audubon Sanctuary in the Santa Ana Mountains of southern California. During this part of the postbreeding season, adult and first-year male Black-chinned Hummingbirds defend foraging territories on the borders of riparian woodlands. To attract a population for manipulations of intrusion pressure, unlimited feeders containing a 0.6 M sucrose solution were placed throughout the study area.

Both experimental and control territories were constructed using nine regulated feeders spaced at 3-m intervals. The feeders were arranged linearly, extending from an area of many suitable perches into an area without perches (Fig. 1). Each feeder was individually supplied by microtubing connected to a 3-ml syringe. Flow rates were controlled with a Sage 355 infusion pump, operating 14 h per day and delivering a 0.6 M sucrose solution at the rate of  $2 \text{ ml} \cdot \text{feeder}^{-1} \cdot \text{day}^{-1}$ . The nine feeders on each territory delivered approximately three times the amount of energy required by a territorial individual per day, based on estimations of energy expenditure during flight (Ewald and Rohwer 1980) and laboratory measurements of oxygen consumption while perching (Lasiewski 1963, Ewald and Carpenter 1978). Our production rates were similar to the maximum measured on natural territories. Kodric-Brown and Brown (1978), for example, found that Rufous Hummingbirds (*Selasphorus rufus*) occasionally defend territories that provide approximately three times their daily energy requirements. Gass (1979) also found that territory quality can vary by a factor of three. Although our production rates may still seem superabundant, intruders obtained such a large percentage of the supplied food that feeders were usually all drained after uninterrupted visits by the owner.

Intrusion pressure on each territory was manipulated by removing or installing additional feeders in a neighboring area, which was out of the owner's view and which lacked perches and was therefore indefensible (Fig. 1). Because we assumed that intruders trespassed to obtain food, intrusion rate should depend on the length of the string of feeders

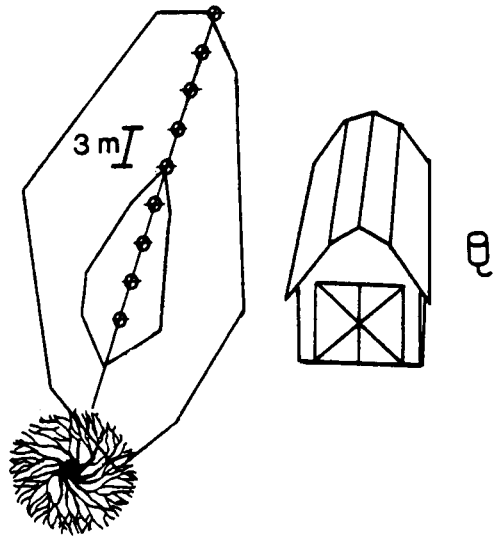


Fig. 1. Diagrammatic representation of experimental site. Polygons represent the largest and smallest areas defended. Feeder symbol represents undefendable feeders used to manipulate intrusion pressure. Circles indicate locations of the nine feeders that were powered by a syringe pump and spaced at 3-m intervals.

rather than on the area of the territory. We therefore quantified intrusion pressure by calculating intrusions per unit length of the string of feeders rather than intrusions per unit area of territory.

Territory size was measured in square meters by means of a grid of flags with which intruder position was estimated at the initiation of a chase. In a few instances, intruders remained within the vicinity of the territories and elicited repeated chases by the owner. These repeated chases were considered continuations of the original chase and were not used in determining territory size. Territory boundaries were determined by connecting the coordinates of the first 40 intruders that elicited a chase, to form a convex polygon.

Data were gathered during observation periods between 0700 and 1100. Observation periods were terminated after 40 chases by an owner. These periods lasted from 20 min to 4 h, depending on intrusion pressure. On the experimental territories, during days of high intrusion pressure, 40 chases were recorded near the beginning and again near the end of the 4-h period. On these days, territory size was determined by alternately assigning chases into two subgroups, each containing 40 intrusions. The territory sizes of these two subgroups were then averaged. This process should have reduced possible effects of time of day.

We observed one territory each day, alternating

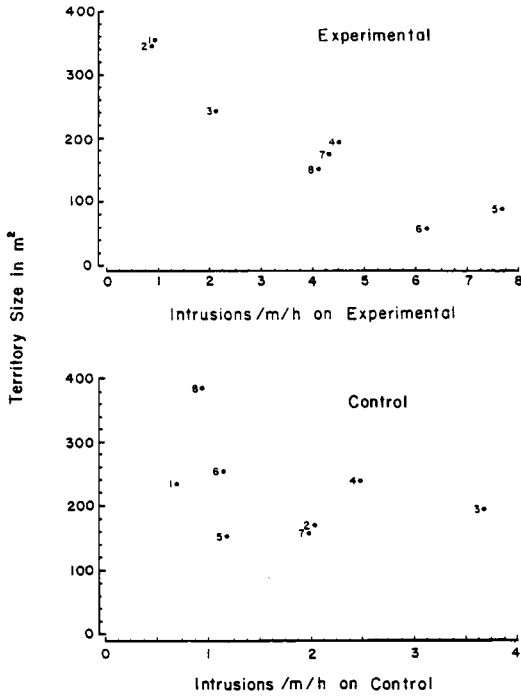


Fig. 2. Relationship between intrusion pressure and territory size on experimental and control territories. Removal of nearby feeders caused increased intrusion pressure in the experimentals. Numbers pair each experimental observation with its control to show that control territory size did not decrease as intrusion pressure was increased on experimentals. Experimental:  $r_s = -0.86$  ( $P < 0.01$ , three different birds); control  $r_s = -0.19$  ( $P > 0.05$ , four different birds).

between a control territory one day and an experimental territory the next. All territory owners were juveniles, and gorget plumages were distinct enough that individuals could be easily differentiated. Following new ownership, each territory was allowed to equilibrate for 2 days before we measured territory size.

Our manipulations of intrusion pressure on the experimental territories resulted in a range of 0.9 to 7.7 intrusions  $\cdot m^{-1} \cdot h^{-1}$ . We maintained a narrower range of intrusion pressure on the control territories, 0.7–3.7 intrusions  $\cdot m^{-1} \cdot h^{-1}$ .

In Fig. 2, the size of experimental territories is shown to have decreased as intrusion pressure increased ( $r_s = -0.86$ ,  $P < 0.01$ ). In response to moderate increases in intrusion pressure, owners were observed to reduce the sizes of their buffer zones around the feeders. During the 2 days of highest intrusion pressure, the focal bird defended as few as

five of the nine feeders, the remainder being defended by a second bird. Each observation period on an experimental territory was paired with a control observation period that occurred on the previous or following day (Fig. 2). This was done to show that the size of control territories did not decrease as intrusion pressure was increased on experimental territories ( $r_s = 0.05$ ,  $P > 0.05$ ). This lack of a correlation between controls and experimental intrusion pressure indicates that the significant correlation among experimentals was due to effects of intrusion pressure rather than to spurious effects; for example, without such controls, one could argue that owners decrease territory size as they become more familiar with their territory.

On the control territories, territory size decreased as intrusion pressure increased, but not significantly, presumably because the range of intrusion pressure was so narrow (Fig. 2). When experimental and control data are combined, territory size decreases significantly in response to increased intrusion pressure ( $r_s = -0.6$ ,  $P < 0.05$ ).

Our assumption that intrusion pressure should be calculated as a linear function does not influence our conclusion that territory size decreased as a result of increased intrusion pressure. Quantifying territory size in terms of area still yields a significant trend for combined data ( $r_s = -0.83$ ,  $P < 0.001$ ), as well as for the experimental territories ( $r_s = -0.98$ ,  $P < 0.001$ ), and a nonsignificant correlation for the control territories.

Our results confirm the prediction that increased intrusion pressure decreases territory size when food is provisioned at a constant rate. Consequently, our results support the hypothesis that food density influences territory size through the intervening variable of intrusion pressure.

Our results are consistent with those of Myers et al. (1979) on wintering Sanderlings and Ewald et al. (1980) on breeding Western Gulls. In our study, however, food was provisioned on the territories at a constant level while intrusion pressure was independently varied. We were therefore assured that our changes in territory size resulted from changes in intrusion pressure rather than from changes in some environmental correlate of intrusion pressure. Clearly, a similar experiment is needed in which intrusion pressure is held constant and food availability varied, thus testing the hypothesis that an increase in food abundance will cause a decrease in territory size when the intermediate variable of intrusion pressure is controlled. Also, it would be valuable to run an experiment similar to ours but with lower food production rates. Such an experiment could test the effects of intrusion pressure on territory size when food is provisioned at rates approximating the daily requirement for a territorial hummingbird.

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## Further Notes on the Juvenal Plumage of the Lesser Nighthawk

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Since the publication of a note on geographic variation in the Lesser Nighthawk (*Chordeiles acutipennis*) (Dickerman 1981), I have encountered the description of a subspecies that was omitted from that manuscript and have received correspondence regarding color phases in the Lesser Nighthawk.

*Chordeiles a. crissale* was described by Miller (1959) from five adults from the upper valley of the Rio Magdalena of Colombia. Its range is within that of the nominate subspecies, an area of confusing juvenal plumages that exhibit two color/pattern variants. The distribution of these variants does not conform to the range of *crissale*, and they do not appear to have well-defined geographic ranges themselves, as do the variants from throughout the rest of the range of the species. Very few specimens are available, however, and additional material is needed.

Regarding color phases, I noted that they were not evident in the series of 13 juvenile *C. a. texensis*. G. S. Grant (North Carolina Museum of Natural History) loaned me two colored slides taken in the Salton Sea area of California in July 1976 and June 1979, which show three juvenile *texensis* that exhibit a great amount of color variation. One slide is of two sib-

lings (found in the same "nest" and quite distant from other nestling nighthawks) that vary little; both are pale with buffy to buffy ochraceous edgings to the dorsal feathers. The other slide is of a young with dramatically darker feather edgings, being nearer deep cinnamon, even when differences in film, shadows, etc. are considered. I re-examined the juvenile *texensis* available in the American Museum of Natural History and would now write: "Juvenile *texensis* exhibit a gradient in the color of the edgings, but the material examined cannot be separated into sharply demarked color phases."

I wish to thank Dr. Grant for loaning me the colored slides.

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