

1987

Effects of Variation in Food Quality on the Breeding Territoriality of the Male Anna's Hummingbird

Donald R. Powers

George Fox University, dpowers@georgefox.com

Follow this and additional works at: http://digitalcommons.georgefox.edu/bio_fac

 Part of the [Biology Commons](#)

Recommended Citation

Powers, Donald R., "Effects of Variation in Food Quality on the Breeding Territoriality of the Male Anna's Hummingbird" (1987).
Faculty Publications - Department of Biology and Chemistry. Paper 18.
http://digitalcommons.georgefox.edu/bio_fac/18

This Article is brought to you for free and open access by the Department of Biology and Chemistry at Digital Commons @ George Fox University. It has been accepted for inclusion in Faculty Publications - Department of Biology and Chemistry by an authorized administrator of Digital Commons @ George Fox University.

EFFECTS OF VARIATION IN FOOD QUALITY ON THE BREEDING TERRITORIALITY OF THE MALE ANNA'S HUMMINGBIRD¹

DONALD R. POWERS²

Department of Biology, San Diego State University, San Diego, CA 92821

Abstract. Thirteen territorial male Anna's Hummingbirds, *Calypte anna*, were observed during the 1981 and 1982 breeding seasons. Breeding territories were large, but size was not determined by energy availability. When a food source (sucrose solution in feeders) was present, the degree to which it was defended was a function of food quality. If a high-quality food source was absent, males did not exhibit the behaviors associated with defending a food source, but breeding territoriality remained intact. Territories were maintained for the entire breeding season even when food quality was varied. The lack of a relationship between the number of chases involving females and dive displays with variations in food quality, along with observations of long territory tenure, suggest that the primary function of the territory is reproductive and that an internal food source is not necessary for its maintenance.

Key words: Territory quality; female choice; exploded lek; energy availability; territory tenure; territory defense.

INTRODUCTION

The availability of energy is important to nectarivorous birds that are maintaining breeding territories because individuals must meet energy requirements as well as achieve reproductive success (Wolf and Stiles 1970, Wolf and Wolf 1976). Energy is obtained mainly from floral nectars (Carpenter and MacMillen 1976b, Feinsinger 1976, Wolf et al. 1976) which are typically 6 to 38% carbohydrate (Percival 1965, Hainsworth 1973, Baker 1975). The availability of floral nectar depends on weather conditions (e.g., Gass and Lertzman 1980) and the flowering seasons of plants (Grant and Grant 1968, Stiles 1973, Gass 1978).

Territories of nonbreeding nectarivorous birds are usually centered on food sources (see Gill and Wolf 1975, Gass 1979, Hixon et al. 1983). There are questions as to what determines optimal territory size, but flower density and intruder pressure seem to be important factors (Gass et al. 1976, Kodric-Brown and Brown 1978, Hixon et al. 1983). Few studies have been conducted on breeding territories, and the relationship between breeding territories and food sources is not well understood. It has been suggested that breeding territories of hummingbirds are established near good food sources whenever possible not only to

provide energy for the males, but also to enhance their reproductive success by attracting females (Wolf and Stiles 1970, Stiles 1973). Tamm (1985) demonstrated that breeding male Calliope Hummingbirds, *Stellula calliope*, display more frequently when energy availability is high. Tamm suggests that display rate may affect the number of feeding attempts by intruders as well as provide females with a mechanism for evaluating males.

Pitelka (1942) suggested that the mating function of hummingbird breeding territories is secondary to the defense of food sources. Stiles (1973), however, showed that although *C. anna* males establish breeding territories around food sources, the territories are maintained for some time after food sources have diminished and that territory size is not strongly correlated with internal food supplies.

This study examines more closely the relationship between energy availability and breeding territoriality of male *C. anna* to determine the extent to which an energy supply inside the territory affects a breeding male's territorial behavior and mating chase frequency.

METHODS

Field observations were carried out between January and May of 1981 and 1982 at the Tucker Wildlife Sanctuary in Modjeska Canyon, Orange County, California and in the adjoining Cleveland National Forest. The primary habitats of the area are mature chaparral with riparian woodland along the stream beds of canyons. Since

¹ Received 19 February 1986. Final acceptance 3 September 1986.

² Present address: Department of Avian Sciences, University of California, Davis, CA 95616.

natural food plants were scarce, the population of approximately 150 hummingbirds was supported mainly by feeders maintained at the sanctuary (Copenhaver and Ewald 1980).

Breeding territories were mapped in 1981, and this information used to select sites for food energy manipulations in 1982. All territories established were in the chaparral regions of the study area. Sites chosen were on slopes facing south or southwest with an adjacent ravine or gully. All sites had many large woody shrubs, usually *Ceanothus*, which offered bare branches that could be used as territorial perches.

Twelve potential sites were identified in the study area; of these, six were randomly chosen for food energy manipulations. Feeders containing 20%-sucrose solution were placed on the selected territories in mid-November, and all twelve were checked daily to determine if males preferentially established breeding territories in the areas with a feeder.

Feeders used were the tubular type (Hainsworth 1973) except that a small piece of rubber tubing was inserted into the glass tubing so that the flow of sugar solution could be controlled with a small clamp. Sugar solution flow rates were regulated at 3.0 ml/hr.

Once a territory was occupied, no data were collected for three weeks while males were establishing themselves (see Stiles 1973). During this period, males may show unusually high levels of energy expenditure (Copenhaver and Ewald 1980). Territory size was measured by plotting the locations of territorial behaviors on a grid, such as the intercept point of chases, sites of aggressive displays, and singing locations of the resident male. Perching locations were recorded and classified according to their frequency of use. Primary perches were those used most frequently and to which a male habitually returned following major territorial activities. Secondary perches were used infrequently but regularly. Incidental perches were those which were used only once or twice during all observations.

Aggressiveness was measured by the frequency and duration of defensive behaviors, mainly chases and dive displays. Defensive chases were divided into two types: high-altitude and low-altitude based on differences noted during preliminary observations. Low-altitude chases were directed towards intruders that attempted to utilize the resources (usually a perch or food source) of a territorial male. High-altitude chases were

evoked by intruders that were simply flying through the territory. I considered chase duration to be an indicator of a male's aggressiveness towards intruders, and the number of chases to represent the intensity of competition for the territory and its resources. The total length of a chase, or of any other timed activity, was measured from when a male left his perch to when he returned.

Because females nest away from the male's territory and copulation occurs near the nesting area (Stiles 1982), assessing mating success directly was not possible. I indirectly assessed female interest in males by determining the number of chases directed towards females and originating on breeding territories. This assessment is reasonable because the courtship sequence begins on the male's territory (Stiles 1982). There are two possible sources of error in this assessment: (1) some chases may be competitive rather than courtship oriented, and (2) males are potentially rejected prior to the conclusion of courtship (Stiles 1982).

Energy manipulations were carried out January to March. Each of the six territories supplied with feeders was observed under experimental and control conditions. Under experimental conditions, the feeders were supplied with one of the following sucrose solutions: 0, 4, 8, 12, 16, or 20% concentration. Under control conditions all feeders received a 20%-sucrose concentration. This control concentration was used because it represents a reasonable average for most common hummingbird plants (see Baker 1975) and was close to the highest concentration found for nectars in the study area based on refractometry (range 13–23%).

The study was conducted in two phases. In the first phase, half of the six territories were randomly selected to be experimentals. Each experimental was provided with one of the concentrations given above. The other half of the territories were given the control concentration. Each territory was then observed for three 3-hr observation periods (07:00 to 10:00). In the second phase, the experimental and control territories were reversed and the treatment repeated. Behavioral observations were always made from the same point.

ANALYSIS

Chase numbers and times collected under the control conditions were analyzed with homo-

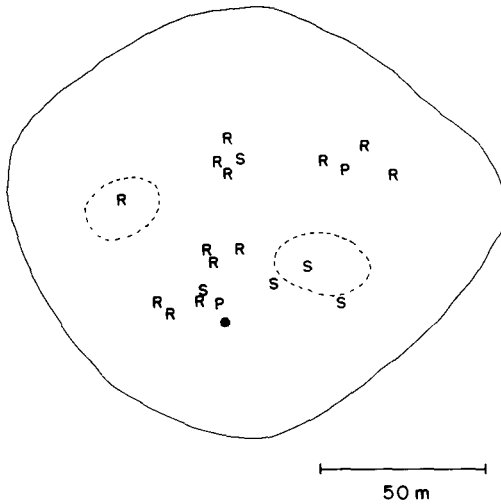


FIGURE 1. Diagrammatic representation of a typical *C. anna* breeding territory (12,800 m²) showing primary perches (P), secondary perches (S), incidental perches (R), feeder location (darkened circle), dive display areas (broken line), and territorial boundary (solid line).

geneity chi-square and two-way ANOVA respectively. All experimental-condition data were analyzed with least squares regression and Pearson's correlation. Statistical significance was assumed if $P < 0.05$.

RESULTS

TERRITORY CHARACTERISTICS

In both years, males established territories in mid-December, consistent with the findings of Williamson (1956) and Stiles (1973). In 1981 all seven territories lacked visible nectar sources. In 1982, however, territories were only established in areas supplied with feeders. Of the 13 territories observed in the two years, 12 were de-

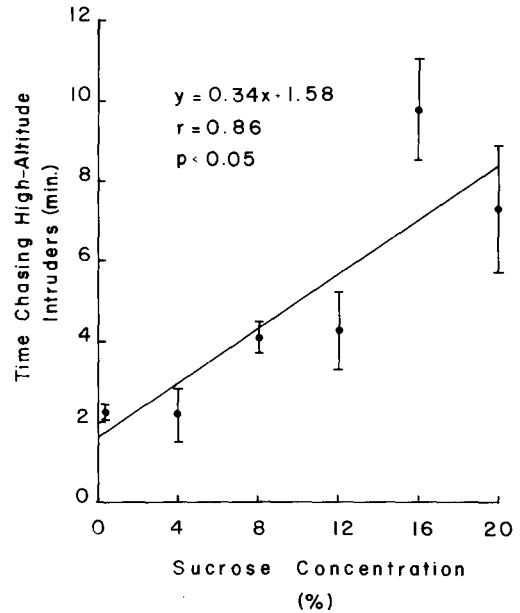


FIGURE 2. The effect of sucrose concentration in experimental feeders on the time *Calypte anna* males spent chasing high-altitude intruders during an observation period.

fended by only one male each until late May. One male disappeared in late March of 1981, and the territory was never reoccupied.

Territories ranged in size from 0.9 ha to 1.3 ha, much smaller than reported by Stiles (1973). Some variability in territory size may be due to differences in the number of behavioral observations used to calculate territory size. However, both the largest and smallest territories measured were defended by birds exhibiting high levels of activity and were well defined. Also, a "core area" (sensu Pitelka 1951) was not evident. Males maintained one to three primary perches, which

TABLE 1. Chase frequency and time spent in chasing low-altitude and high-altitude intruders by *Calypte anna* males during the control state.

Territory no.	Sucrose conc. (%)	High-altitude chases		Low-altitude chases	
		No./hr	Duration (min/chase)	No./hr	Duration (min/chase)
1	20	7.2 ± 0.7	0.29 ± 0.03	2.8 ± 0.5	1.05 ± 0.11
2	20	6.9 ± 1.3	0.26 ± 0.08	3.1 ± 0.2	0.97 ± 0.18
3	20	7.6 ± 1.5	0.30 ± 0.05	2.8 ± 0.2	0.93 ± 0.14
5	20	6.2 ± 3.0	0.35 ± 0.11	3.1 ± 0.7	1.01 ± 0.22
9	20	7.0 ± 2.6	0.37 ± 0.13	3.5 ± 1.7	0.69 ± 0.06
10	20	8.8 ± 1.3	0.29 ± 0.02	3.2 ± 0.8	1.04 ± 0.01

Values are averaged from three 3-hr observation periods for each bird and reported as the mean ± 1 SD.

TABLE 2. Chase frequency and time spent chasing high-altitude and low-altitude intruders by *Calypte anna* males during the experimental state.

Territory no.	Sucrose conc. (%)	High-altitude chases			Low-altitude chases		
		No./hr*	No./hr**	Duration (min/chase)	No./hr*	No./hr**	Duration (min/chase)
9	0	1.5 ± 0.7	1.8 ± 0.9	0.43 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.00 ± 0.00
3	4	2.2 ± 0.7	2.6 ± 0.5	0.33 ± 0.12	0.3 ± 0.0	0.4 ± 0.0	0.90 ± 0.50
2	8	4.0 ± 0.3	4.2 ± 0.3	0.34 ± 0.04	0.9 ± 0.5	0.9 ± 0.5	0.62 ± 0.34
5	12	5.3 ± 0.9	5.5 ± 0.5	0.27 ± 0.02	1.6 ± 0.2	1.6 ± 0.2	0.77 ± 0.21
1	16	9.5 ± 2.4	9.6 ± 2.6	0.36 ± 0.13	2.0 ± 0.6	2.0 ± 0.6	0.70 ± 0.12
10	20	7.1 ± 1.2	7.1 ± 1.2	0.33 ± 0.02	2.9 ± 0.7	2.9 ± 0.7	1.07 ± 0.16

* Values are averaged from three 3-hr observation periods for each bird and reported as the mean ± 1 SD.

** Values are averaged from the total time the bird was on his territory during each of the three 3-hr observation periods for each bird and reported as the mean ± 1 SD.

were not necessarily in close proximity to one another (Fig. 1). Males often initiated territorial behaviors, such as singing, dive displays, and chases, from secondary perches. Dive displays were preferentially performed in specific areas of many territories, but these areas should not be confused with a core area since they were not necessarily associated with a food source or primary perch and were often at the outer boundaries of the territory.

For the most part, breeding territories were on slopes facing south or southwest. Vegetation was dense at the territories' center and thinned out towards the perimeter. Most of the vegetation was low except for the primary perches, which were elevated giving the male a clear view of his territory. Primary perches were usually on the upper exposed branches of *Ceanothus cuneatus*, *Quercus dumosa*, and in the inflorescences of *Yucca whipplei*.

AGGRESSIVE INTERACTIONS

Intruders that were simply passing through a territory usually flew at altitudes greater than 25 m and on some occasions as high as 80 m. Although these intruders were chased, such chases were usually short in duration and distance lasting 0.3 to 0.4 min. High-altitude chases were less intense than low-altitude chases in that the male flew slowly towards the intruder and rarely vocalized. Chases typically ended at the territory boundary, often with the intruder being intercepted by the neighboring male. This possibly cooperative effort was also observed by Stiles (1973). If the intruder was a female this interaction might be interpreted as competition for a mate. High-altitude chases were most often initiated from primary perches. Intruders seemed to be observed from great distances, but were intercepted at a

point which appeared to result in the shortest flight even if it allowed the intruder to enter the territory.

Under control conditions no statistically significant difference was observed between males for the number of high-altitude chases per hour or total chasing time per hour. The mean value for all territories was 7.0 chases/hr, requiring 0.31 min/chase (Table 1). During the experimental phase the mean chase duration for all males did not differ statistically from the control, but the number of chases per hour of observation increased with sucrose concentration ($r = 0.91$, $df = 4$, $P < 0.05$; Table 2) as did the number of chases per hour each male was on his territory ($r = 0.90$, $df = 4$, $P < 0.05$; Table 2), so that males with a better energy supply devoted more time to chasing ($r = 0.86$, $df = 4$, $P < 0.05$; Fig. 2).

Low-altitude chases were intense and appeared to involve flight speeds exceeding those of high-altitude chases. They were executed close to the ground, and were accompanied by strong vocalizations until the last few seconds. Intruders were often intercepted at or near a male's food source or perching location. Chases lasted as long as 1.0 min and extended over great distances, often making the chase impossible to observe in its entirety. This sometimes necessitated the assumption that chases were continuous during brief periods when the birds were out of sight.

Under the control conditions (Table 1), males did not differ statistically in the number of low-altitude chases or in the time spent in them. Males spent an average of 3.0 min/hr conducting low-altitude chases, which is not significantly different from the total time budgeted for high-altitude chases, but increases in chase duration (Table 1) and intensity of low-altitude chases may indicate higher energetic costs.

TABLE 3. Time spent off territory, mating chase frequency, and time spent on mating chases by *Calypte anna* males during the control state.

Territory no.	Time off territory (min/hr)*	Mating chases	
		(No./hr)*,**	(min/hr)*,**
1	0.4 ± 0.4	0.6 ± 0.2	1.2 ± 0.4
2	0.3 ± 0.2	0.2 ± 0.2	0.7 ± 0.7
3	0.0 ± 0.0	0.7 ± 0.3	2.5 ± 2.0
5	0.3 ± 0.3	0.9 ± 0.2	2.8 ± 1.0
9	0.1 ± 0.1	0.2 ± 0.2	1.0 ± 0.9
10	0.2 ± 0.2	0.3 ± 0.0	1.5 ± 0.1
Mean		0.48	1.62

* Values are averages from three 3-hr observation periods for each bird.
 ** These data represent data from chases which are assumed to be mating and not competitive.

During experimental conditions the number of low-altitude chases decreased as sucrose concentrations decreased ($r = 0.99$, $df = 4$, $P < 0.05$). The level of competition appeared to be strongly influenced by the amount of sugar in the feeder because the number of chases per hour increased with sucrose concentration ($r = 0.99$, $df = 4$, $P < 0.05$; Table 2). This differs from breeding Calliope Hummingbirds whose chase frequency remained constant when energy availability was changed (Tamm 1985). Unlike durations of high-altitude chases, duration of low-altitude chases decreased as sucrose concentration decreased ($r = 0.73$, $df = 4$, $P < 0.05$; Table 2). As chase duration decreased, the chases became less intense and vocalizations became irregular. Reductions in both chase duration and number strengthens the relationship between sucrose concentration and time spent in low-altitude chases ($r = 0.93$, $df = 4$, $P < 0.05$; Fig. 3).

Dive displays appeared to be, as Stiles (1982) suggested, an aggressive behavior. However, because display frequency and duration showed no

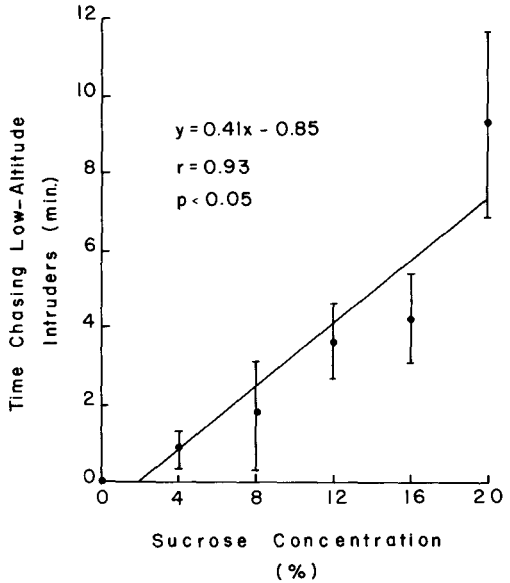


FIGURE 3. The effect of sucrose concentration in experimental feeders on the time *Calypte anna* males spent chasing low-altitude intruders during an observation period.

relationship to sucrose concentration, the function of this aggression in Anna's Hummingbird was unclear. This is different from breeding Calliope Hummingbirds which increase display frequency when more food is made available (Tamm 1985). In this study hummingbirds, especially females, were not common objects of display. Intruding males that succeeded in perching in a territory were displayed over repeatedly, but more than 80% of the displays were directed towards other species of birds, primarily the Scrub Jay, *Aphelocoma coerulescens*. On some occasions the birds appeared to be displaying over an empty bush.

TABLE 4. Time spent off territory, mating chase frequency, and time spent on mating chases by *Calypte anna* males during the experimental state.

Territory no.	Sucrose conc. (%)	Time off territory (min/hr)*	Mating chases	
			(No./hr)*,**	(min/hr)*,**
9	0	10.4 ± 0.6	0.1 ± 0.2	0.2 ± 0.4
3	4	8.1 ± 1.5	0.3 ± 0.3	0.8 ± 0.8
2	8	3.4 ± 0.2	0.3 ± 0.3	0.9 ± 0.9
5	12	1.9 ± 0.8	0.9 ± 0.2	2.9 ± 0.4
1	16	0.6 ± 0.3	0.3 ± 0.3	0.7 ± 0.6
10	20	0.2 ± 0.2	0.2 ± 0.2	0.7 ± 0.7
Mean			0.35	1.03

* Values are averages from three 3-hr observation periods for each bird.

** These data represent data from chases which are assumed to be mating and not competitive.

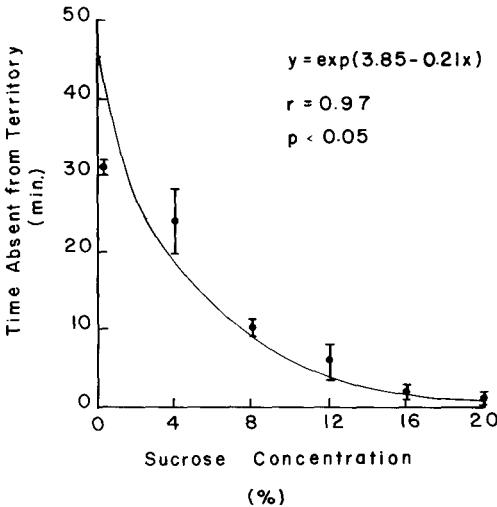


FIGURE 4. The effect of sucrose concentration in experimental feeders on the time *Calypte anna* male spent off their territories during an observation period.

TIME OFF TERRITORY

Males under the control condition never spent more than 2.0 min off their territories for reasons unrelated to chases during a single 3-hr observation period (Table 3). When sucrose concentrations were lowered, the amount of time spent off territories increased dramatically (Fig. 4), presumably because the males needed to search for food. Tamm (1985) observed a similar pattern for breeding Calliope Hummingbirds. During one observation period, male 9, with a feeder containing 0% sucrose, was off his territory 17.3% of the total time (Table 4). This is comparable to the 17 to 20% of time spent off-territory by males without feeders during preliminary observations in 1981. Even though males with low sucrose concentrations were away from their territories for long periods of time, they remained territorial.

MATING BEHAVIOR

Few females observed entered a male's territory without engaging in courtship behavior. No female was ever seen attempting to feed at a male's feeder. Natural nectar sources may provide some visual cue which feeders lack, but in this study there was no evidence that evaluation of food quality by females was taking place.

The portions of courtship behavior observed were very similar to those described by Bent (1940) and Stiles (1982). The mechanics of chases

occurring during courtship closely resembled those of low-altitude chases. Because copulation takes place out of the male's territory (Stiles 1982) it was impossible to observe the entire chase. Males leaving on chases of females were sometimes gone for several minutes.

If high quality food sources attract females, the males in these territories should have the most mating opportunities. This was not the case. There was no statistically significant relationship between numbers of chases involving females or time devoted to such chases and sucrose concentration (Table 4).

DISCUSSION

Recent studies of breeding territoriality in the male *C. anna* under natural conditions have suggested that a high quality food source contributes to the male's mating success (Stiles 1973, 1982). However, observations of territory size, tenure, and female activity in this study indicate that an energy source in the breeding territory may not be necessary for breeding success.

It is not surprising that areas with rich energy sources were utilized first by breeding male Anna's Hummingbirds. Due to the spatial and temporal variability of natural nectar sources, a territory established for the defense of a nectar source should, at least in part, be a function of flower density (see Gill and Wolf 1975, Gass et al. 1976, Kodric-Brown and Brown 1978). However, unlike the *C. anna* observed by Stiles (1973), breeding territories were occupied for long periods regardless of energy availability. Males holding energy-poor territories utilized the sanctuary feeders or intruded on the territories of other males. The reliability of feeders at the sanctuary may make having a food source in the territory less important.

The time and energy expended on territory establishment indicate the importance of long-term occupation of breeding territories. Feeding territories may be established in a matter of hours (Copenhaver and Ewald 1980), but establishment of *C. anna* breeding territories requires as much as three weeks. Stiles (1973), who first observed this pattern, suggested that this lengthy establishment period may require males to begin breeding behavior earlier than females.

Generally, the size of a feeding territory is negatively correlated with the energy available per unit area (Gill and Wolf 1975, Gass et al. 1976, Kodric-Brown and Brown 1978, Gass 1979, Hix-

on et al. 1983), and when energy availability falls below threshold levels territoriality can deteriorate (Carpenter and MacMillen 1976a, Ewald and Carpenter 1978, Kodric-Brown and Brown 1978). However, in this study breeding territories remained large regardless of sugar concentration, and more importantly, at no time did any of the males become nonterritorial. Breeding males may sacrifice net foraging gains to increase frequencies of mating.

In my population a male's food source did not seem to play a major role in attracting females because none of the breeding territories contained a significant number of flowers. Gass and Lertzman (1980) found that when food resources were removed from an area, nonbreeding Rufous Hummingbirds, *Selasphorus rufus*, stopped using the area. If food sources on breeding territories are critical to *C. anna*, similar results should have been observed for territories supported with low concentrations of sucrose, especially since the males have the added pressures of being reproductively successful. In addition, the females observed did not benefit energetically from the male's food source (see also Stiles 1971, 1982). In breeding systems such as this, females presumably select males on some measure of fitness, but it is unclear as to how fitness could be tied to a resource as variable as flower nectar in a long-term territorial system. It should be pointed out, however, that the *C. anna* population used in this study has been feeder-dependent for several years. Utilization of a reliable, artificial food source for generations may have had a profound effect on the relationship between the breeding system and the food source of the Anna's Hummingbird.

FOOD QUALITY AND AGGRESSIVENESS

Competition was dependent upon the quality of the male's food source. The strength of this relationship and the lack of successful intrusions by competing males made evaluation of a territory owner's aggressiveness difficult, however. Two factors seem to be indicators of aggressiveness. First, it is unlikely that the rate of high-altitude intrusion was affected by the quality of the food source. Rather, reduction in the number of chases probably resulted from males in energy-poor territories not responding to as many high-altitude intruders. High-altitude intruders which were not chased appeared to be more frequent on energy-poor territories. This lack of response

could be a means of conserving energy. Secondly, Copenhaver and Ewald (1980) suggest that longer chases deter competitive intruders from returning, rather than just increasing the cost of intrusions. Increasing the duration of low-altitude chases may result in long-term energy savings for males on energy-rich territories.

Chase length was not a factor in high-altitude chases, which did not appear to be energetically expensive relative to low-altitude chases and probably functioned simply to reassert territorial ownership. However, energy-dependent variation in chase length was seen frequently in low-altitude chases. This behavior is similar to that seen in feeding territories (Ewald and Carpenter 1978), indicating that aggressiveness is important to the defense of food sources inside the territory. This similarity suggests that when food sources are present the breeding territory may indeed, as Pitelka (1951) suggested, function secondarily as a feeding territory. The presence of food, under these conditions, is not a requirement for a breeding territory of *C. anna*, but a high quality food supply in the territory may increase its net benefits (Wolf 1978).

FOOD QUALITY AND MATING SUCCESS

Three aspects of this study indicate that a male's mating success is independent of food supply under the conditions of this study: (1) a food source within the breeding territory was not a requirement for territory maintenance; (2) females made no obvious attempt to feed at a male's food source; and (3) no relationship was detected between the level of aggressiveness and a male's involvement in courtship behavior.

Food quality may have an indirect effect on a male's mating activity by determining the time spent off his territory. Males with lower sucrose concentrations spent much more time off their territories than those with high concentrations. Because females solicit males (Stiles 1982), males spending long periods off their territories may lose opportunities to mate.

Males that must leave their territories to feed probably have higher foraging costs than those with food supplies in their territories (Wolf 1978). If the increased foraging costs are not offset by reductions in the cost of territorial defense then the *C. anna* breeding system may suffer a net loss in energetic benefits. This is not unknown in nature. Feldmeth (1983), in a study on trout and pupfish, observed more intense agonistic and

courtship behavior than available food resources should have allowed.

THE MATING SYSTEM

The breeding behavior of male *C. anna* closely resembles that of "promiscuous species" (Pitelka et al. 1974), in which males form leks, in this case an "exploded lek" because males are widely separated. Exploded leks usually develop when food resources are widely dispersed and difficult to defend (Payne and Payne 1977), as was the case in the present study prior to the introduction of feeders. Distribution of breeding territories did not appear to be a function of food availability. The distribution of territories in 1981, when territories were without feeders, was similar to the distribution of territories in 1982 when feeders were used. The establishment of breeding territories on slopes above the nesting areas may be advantageous in that it offers easy access of females to males.

The concept of an exploded lek also suggests an auditory function for the dive display in addition to its visual function (Foster 1983). The "squeak" produced at the bottom of the display is the only sound produced by *C. anna* that could be heard throughout the study area. This may allow the display to function visually at short range and acoustically at long range.

The behavioral and morphological characteristics of *C. anna* are consistent with those of other lek species (see Welty 1982). These traits include absence of a pair bond, nonparticipation of males in nesting, nesting of females away from male territories, strong sexual dimorphism, dynamic displays (Stiles 1982, also see Snow 1974), complex vocalizations (Stiles 1982; also see Snow 1974, 1977), and feather structures modified for the purpose of producing sound (Rodgers 1940, Stiles 1982, Skutch 1949, Willis 1966). The major deviation from typical lek behavior is that copulation occurs outside the male's territory (Stiles 1982), whereas in other lek systems copulation occurs on the lek (see Pitelka et al. 1974, Snow 1974, Wittenberger 1981). Because courtship behavior begins in the male's territory, however, this point may be unimportant.

CONCLUSIONS

The results of this study, compared to those of Pitelka (1951) and Stiles (1971, 1973, 1982), indicate that males of *C. anna* modify their territorial breeding behavior in response to variation

in food resource distribution. The willingness of males to occupy breeding territories continually under varying conditions of energy availability suggests that mating success is the primary function of territoriality and that an internal food supply in the breeding territory may be advantageous, but not a necessity. Females in this study were not attracted to a male on the basis of his territory's food quality indicating that other factors are involved. Breeding territories were established by *C. anna* males on canyon slopes and appear to be loosely aggregated into exploded leks. The latter feature needs further study. When internal food supplies were available feeding territories were defended within breeding territories.

ACKNOWLEDGMENTS

My thanks to George W. Cox, Wesley W. Weathers, Frank A. Pitelka, Paul W. Ewald, F. Gary Stiles, and Ann Brice for commenting critically on earlier versions of the manuscript. Field data were collected with the help of Melissa Foster, Jon Francine, Marilyn Hildebrand, Debbie Jackson, Raphael Payne, Theodora Powers, Kurt Shanebeck, and Doyle Siemens. The California State University, Fullerton, provided generous use of the facilities at the Tucker Wildlife Sanctuary. Invaluable technical assistance was provided by Ray Munson, Raphael Payne, and Theodora Powers. This project was done in partial fulfillment of the requirements for the Master of Science degree at San Diego State University.

LITERATURE CITED

- BAKER, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* 7:37-41.
- BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U. S. Nat. Mus. Bull. No. 176.
- CARPENTER, F. L., AND R. E. MACMILLEN. 1976a. A threshold model of feeding territoriality and a test with an Hawaiian honeycreeper. *Science* 194:639-642.
- CARPENTER, F. L., AND R. E. MACMILLEN. 1976b. Energetic cost of feeding territories in an Hawaiian honeycreeper. *Oecologia* 26:213-223.
- COPENHAVER, C., AND P. W. EWALD. 1980. Cost of territory establishment in hummingbirds. *Oecologia* 46:155-160.
- EWALD, P. W., AND F. L. CARPENTER. 1978. Territorial responses to energy manipulations in the Anna Hummingbird. *Oecologia* 31:277-292.
- FEINSINGER, P. 1976. Organization of a tropical guild of nectarivorous birds. *Ecol. Monogr.* 46:257-291.
- FELDMETH, C. R. 1983. Cost of aggression in trout and pupfish, p. 117-138. *In* W. P. Aspey and S. L. Lustick [eds.], *Behavioral energetics: survival in vertebrates*. Ohio State Univ. Press, Columbus.
- FOSTER, M. S. 1983. Disruption, dispersion, and

- dominance in lek-breeding birds. *Am. Nat.* 122: 53-72.
- GASS, C. L. 1978. Rufous Hummingbird feeding territoriality in a suboptimal habitat. *Can. J. Zool.* 56:1535-1539.
- GASS, C. L. 1979. Territory regulation, tenure, and migration in rufous hummingbirds. *Can. J. Zool.* 57:914-923.
- GASS, C. L., G. ANGEHR, AND J. CENTA. 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. *Can. J. Zool.* 54:2046-2054.
- GASS, C. L., AND K. P. LERTZMAN. 1980. Capricious mountain weather: a driving variable in hummingbird territorial dynamics. *Can. J. Zool.* 58: 1964-1968.
- GILL, F. B., AND L. L. WOLF. 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56:333-345.
- GRANT, K. A., AND V. GRANT. 1968. Hummingbirds and their flowers. Columbia Univ. Press, New York.
- HAINSWORTH, F. R. 1973. On the tongue of a hummingbird: its role in the rate and energetics of feeding. *Comp. Biochem. Physiol. A. Comp. Physiol.* 46:65-78.
- HIXON, M. A., F. L. CARPENTER, AND D. C. PATTON. 1983. Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. *Am. Nat.* 122:366-391.
- KODRIC-BROWN, A., AND J. H. BROWN. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. *Ecology* 59:285-296.
- PAYNE, R. B., AND K. PAYNE. 1977. Social organization and mating success in local populations of village indigobirds, *Vidua chalybeata*. *Z. Tierpsychol.* 45:113-173.
- PERCIVAL, M. S. 1965. Floral biology. Pergamon Press, Oxford.
- PITELKA, F. A. 1942. Territoriality and related problems in North American hummingbirds. *Condor* 44:189-204.
- PITELKA, F. A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. *Ecology* 32:641-661.
- PITELKA, F. A., R. T. HOLMES, AND S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in arctic sandpipers. *Am. Zool.* 14:185-204.
- RODGERS, T. L. 1940. The dive note of the Anna Hummingbird. *Condor* 42:86.
- SKUTCH, A. F. 1949. Life history of the Yellow-thighed Manakin. *Auk* 66:1-24.
- SNOW, B. K. 1974. Lek behavior and breeding of Guy's Hermit Hummingbird *Phaethornis guy*. *Ibis* 116:278-279.
- SNOW, B. K. 1977. Territorial behavior and courtship of the Three-wattled Bellbird. *Auk* 94:623-645.
- STILES, F. G. 1971. Time, energy, and territoriality of the Anna Hummingbird. *Science* 173:818-820.
- STILES, F. G. 1973. Food supply and the annual cycle of the Anna hummingbird. *Univ. Calif. Publ. Zool.* 97:1-109.
- STILES, F. G. 1982. Aggressive and courtship displays of the male Anna's Hummingbird. *Condor* 84: 208-225.
- TAMM, S. 1985. Breeding territory quality and agonistic behavior: effects of energy availability and intruder pressure in hummingbirds. *Behav. Ecol. Sociobiol.* 16:203-207.
- WILLIAMSON, F. S. 1956. The molt and testis cycle of the Anna Hummingbird. *Condor* 58:342-366.
- WITTENBERGER, J. F. 1981. Animal social behavior. Duxbury Press, Boston.
- WELTY, C. J. 1982. The life of birds. 3rd ed. Saunders College Pub., San Francisco.
- WILLIS, E. O. 1966. Notes on a display and of the Club-winged Manakin. *Auk* 83:475-476.
- WOLF, L. L. 1978. Aggressive social organization in nectarivorous birds. *Am. Zool.* 18:651-664.
- WOLF, L. L., AND F. G. STILES. 1970. Evolution of pair cooperation in a tropical hummingbird. *Evolution* 24:759-773.
- WOLF, L. L., F. G. STILES, AND F. R. HAINSWORTH. 1976. Ecological organization of a highland tropical hummingbird community. *J. Anim. Ecol.* 45: 349-379.
- WOLF, L. L., AND J. S. WOLF. 1976. Mating system and reproductive strategy of Malachite Sunbirds. *Condor* 78:104-107.