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24. Supported by NSF grants GA25400 and GV28305 (Office of Polar Programs).

30 April 1971; revised 28 June 1971 ■

Time, Energy, and Territoriality of the Anna Hummingbird (Calypte anna)

Abstract. *The male Anna Hummingbird accommodates seasonal changes in energy demands by varying its allocation of time and energy among different activities; total energy expenditures change relatively little. Augmented territorial defense during the breeding season is made possible by increased feeding efficiency due to the availability at this time of very nectar-rich flowers.*

A study of the way an organism budgets its available time and energy can provide valuable data for an ecological analysis of its behavior. Hummingbirds, because of their small size, are faced with relatively great problems of heat loss and energy balance. Time and energy studies of hummingbirds are therefore of particular ecological interest. Hummingbirds are also ideal subjects for the translation of time budgets into energy budgets since their active day is spent at essentially two distinct metabolic levels, perching and flight. (Most hummingbirds are incapable of terrestrial locomotion.)

Pearson (*1*) was the first to use physiological data to quantify the metabolic costs of various activities of a wild bird, a nonbreeding male Anna Hummingbird (*Calypte anna*). My objective in this report is to extend this analysis to other times of year and other ecological contexts, in order to determine the effects of reproduction and territoriality on the time and energy budget of the male Anna Hummingbird.

The bird observed by Pearson was holding a feeding territory; defense of flowers by male Anna Hummingbirds is common during the nonbreeding season (*2*). The size of the feeding territory varies with the density and nectar production of the flowers, and the level of competition (*3*). Most feeding territories are only a few square meters in extent; the surrounding area is not defended, and intruders are seldom pursued far beyond the bounds of the territory (*2*). During the breeding season male *C. anna* hold breeding territories consisting of a central "core area" of about 0.1 ha, and a surrounding "buffer zone" of up to 4 to 6 ha (*2, 4*). In breeding territories the area itself is defended rather than a food source, although the distribution of flowers is apparently important in the choice of a territory site by male *C. anna*. Breeding males engage in advertising flights, display dives, and frequent long chases in defense of their territories (*4*). In energetic terms, breeding territories thus appear to be much more expensive to defend than feeding territories.

Field observations were made in the Santa Monica Mountains, Los Angeles County, California. Breeding males were studied in February and March 1967, January through April 1968, and March 1969; males on feeding territories were observed in October 1968 (*5*). The basic method was continuous observation of wild birds for periods of from several hours up to a full day. The time of day and the length and nature of all bouts of activity were recorded. Activities were classified as perching (*P*), feeding at flowers (*F*), insect-catching by gleaning or hawking (*ic*), territorial aggression (*A*), miscellaneous flying (*f*), and out of contact (*ooc*). This last category includes time that the bird was out of my sight, hearing, or both, and almost always involved long flights beyond the bounds of the territory. Data on ambient (T_A) and black-bulb (T_{BB}) temperatures (*6*) and weather conditions were taken every 15 minutes in the field.

To obtain an accurate and meaningful time budget, one must study a bird whose activities are highly localized and visible, and all of whose territory and the surrounding area can be efficiently scanned. The abundances of flowers present in the territories of individual male *C. anna* differ greatly, and hence there are differences in the amount of time the birds must spend feeding elsewhere, often at considerable distances (*2*). I was unable to evaluate feeding activity for most males that fed to any considerable extent outside of their territories. Of necessity, I was restricted to intensive observation of those few individuals that met all these requirements. I obtained 69 hours of observations, including

two full days, on one breeding male *C. anna*, and some 25 hours on six other males in the local population (*7*). Much of the latter observations are comparatively unreliable because of the large amount of time these birds were out of contact. I also obtained 16 hours of observations on two males holding feeding territories for comparison with Pearson's data (*1, 8*). Generalizations derived from data on so few individuals must be viewed with caution but are potentially useful in suggesting directions for future research.

Energy budgets were obtained by calculating the caloric equivalents of perching and flight. Perching metabolism was calculated by Pearson's method (*1, 9*). Flight metabolism was assumed to be 50 ml of O_2 per gram per hour or 0.018 kcal/min; forward and hovering flight were assumed to be equally expensive metabolically (*10*).

Under comparable weather conditions, the proportion of time spent in flight for birds on breeding territories is quite similar to that for birds on feeding territories (Figs. 1 and 2). High ambient temperatures and strong insolation are accompanied by a decrease in flying regardless of the type of territory and the time of year. For the data of Fig. 1, significant negative correlation exists between total flying time and both T_A ($r = -.83$, $p < .001$) and T_{BB} ($r = -.67$, $p < .01$).

Although the total amount of flying activity remains fairly stable, the allocation of time and energy differs markedly between breeding and feeding territoriality (Figs. 1 and 2). Depending on the individual and the weather, as much as four times as much time and energy are expended in defense of a breeding territory as in the defense of a feeding territory. This increase in aggressive activity by breeding birds coincides with a marked decrease in feeding activity at flowers, as is shown by the ratios between aggressive and feeding activities for different males in Fig. 1. At comparable temperatures, the $A : F$ ratio for breeding birds is three to five times that for nonbreeding birds. There is little difference in insect-catching activity between breeding and feeding territories. Breeding birds are thus increasing energy expenditures for territoriality, but are actually decreasing the time devoted to energy intake.

Breeding males spend different proportions of their time feeding and fighting, with the time spent in each activity dependent in large part on the quality of the nectar supply on territory. Individuals controlling better food resources must spend less time feeding, but often defend their territories more frequently (*2*). All the males in Fig. 1 except one controlled enough flowers so that they could do all their feeding on territory. Male 68-Y held a poorer territory than the other males shown in Fig. 1 and did considerable feeding at a small *Eucalyptus* tree 200 m away. (This bird was the only one I studied whose off-territory feeding area could be observed from the vicinity of the territory.) The $A : F$ ratio for bird 68-Y is lower than for other males at similar temperatures (Fig. 1).

To remain in energy balance, breeding birds must be accumulating more energy per unit feeding time than birds on feeding territories. The flowers most frequently used by breeding *C. anna* males are *Ribes speciosum* and *Eucalyptus globulus*. The former is the most nectar-rich of native food plants, the latter the most nectar-rich of introduced ones (*2*). The high nectar production of these flowers probably makes possible the requisite increase in feeding efficiency by breeding birds. Indeed, it is probable that a territorial system as energetically demanding as that of the breeding male *C. anna* could not have evolved without a rich nectar source such as *Ribes*. I have argued elsewhere (*2*) that female *C. anna* choose to mate with males on the best territories (that is, those with the

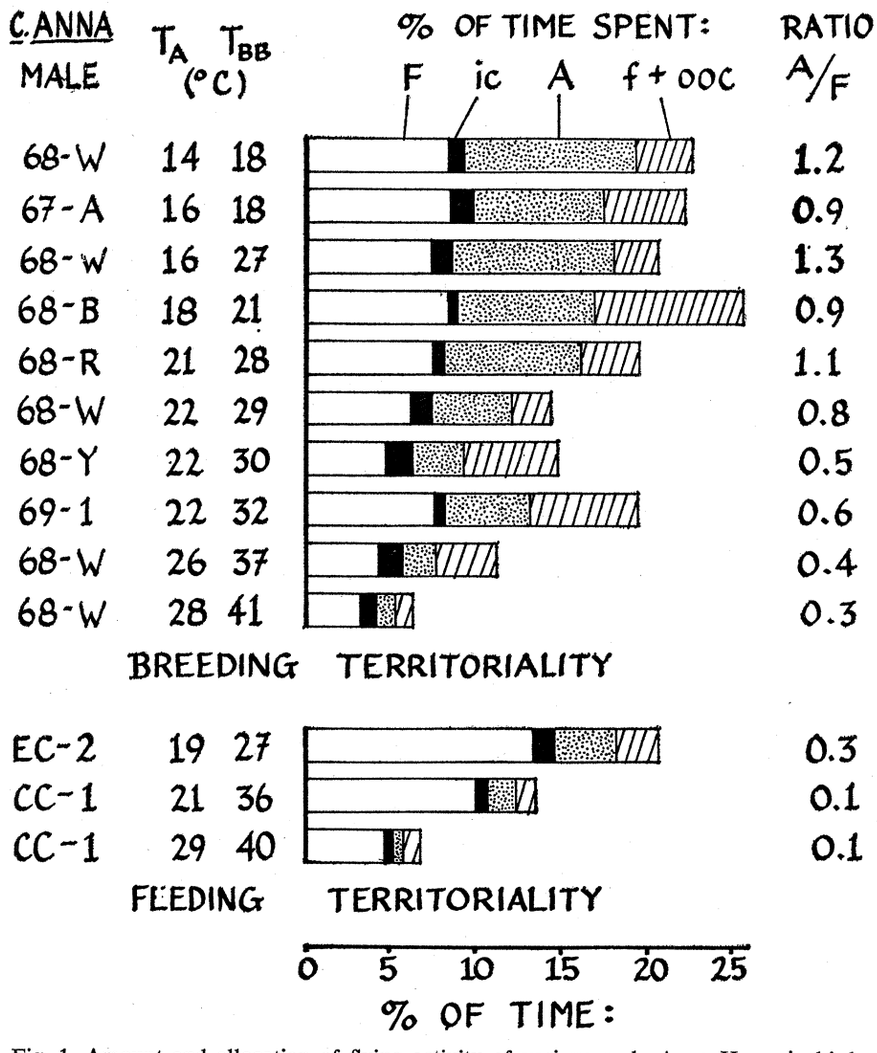

Fig. 1. Amount and allocation of flying activity of various male Anna Hummingbirds, on breeding and feeding territories. Observation periods were 2 to 4 hours in length, in late morning or early afternoon; observation periods in which time out of contact (*ooc*) made up more than 50 percent of all flying time are excluded. Observation periods are arranged approximately in order of increasing ambient (T_A) and black-bulb (T_{BB}) temperatures, to show the depressing effect of high temperature on flying activity. *F*, Feeding at flowers; *ic*, insect catching; *A*, territorial aggression; *f*, miscellaneous flying.

most *Ribes*), and competition between males for these territories is most intense. Ability in territorial defense is thus an important component of reproductive fitness in the male *C. anna*, and this characteristic may have influenced the evolution of such a strenuous territorial system.

An organism can accommodate the increased seasonal demands of reproduction and territoriality by increasing its total energy expenditures, or by changing the allocation of time and energy to different activities while maintaining total energy expenditures relatively constant (*11*). Studies of male passerines indicate that they use primarily the first strategy (*11, 12*), whereas the male Anna Hummingbird appears to use primarily the second. Greater availability of food is critical for both strategies but especially for the second, where increased territorial activity comes at the expense of feeding time. The stationary, conspicuous nature of flowers and their continued secretion of nectar over periods of several hours greatly enhance their value as a food resource. Insects, although important nutritionally, contribute relatively little to the total energy budget of male Anna Hummingbirds. Similarly, insectivorous passerines may not be able to increase their feeding efficiency as greatly as hummingbirds can because insects are a less predictable food source than nectar (*13*).

The fact that all of a hummingbird's major activities involve flight, and are therefore relatively expensive energetically, may partly explain why no overall increase in flying with breeding occurs in male *C. anna*. A ratio of flight to perching time of 1 : 5 or 1 : 6 may be the most efficient long-term operating condition for a hummingbird not in the special physiological state associated with migration. A "two-gear" metabolic strategy—bouts of intense activity alternating with quiescent periods—is also an efficient one for a small mammalian homoiotherm (*14*).

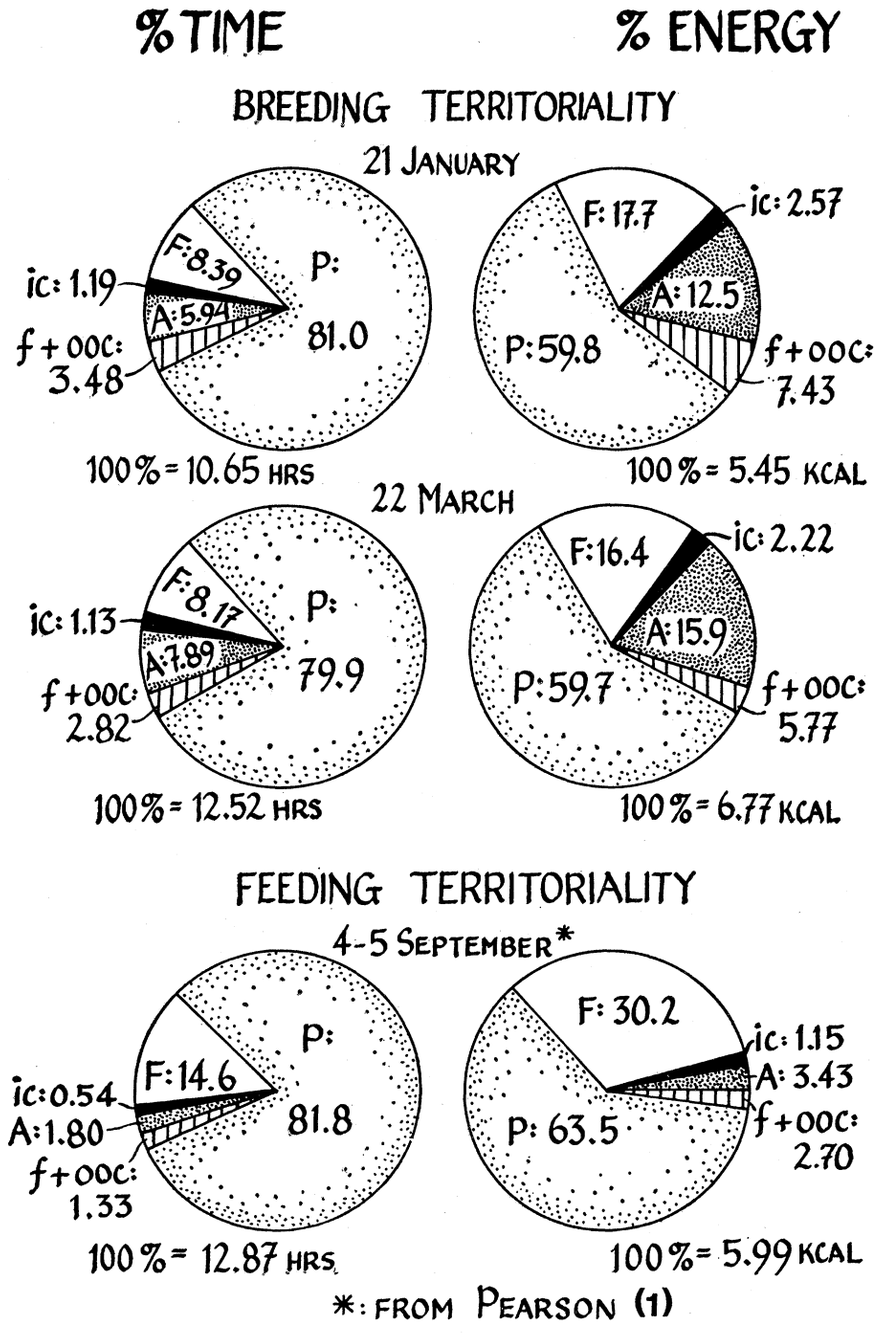

Fig. 2. Percent of total active day (dawn to dusk) spent at various acitvities by one male *C. anna* on breeding territory on two different days, and by one male *C. anna* on feeding territory [average of two consecutive days; data from Pearson (*1*)]. Weather conditions appear quite similar for all 4 days (sunny, with a daily temperature range of 12° to 25°C). *P*, perching; other abbreviations used are the same as those given in Fig. 1.

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6. Black-bulb temperature was taken with a Schultheis thermometer encased in a glass test tube painted with flat black enamel, placed in full sun and out of the wind. Although at best an approximation to true blackbody temperature, these data are a useful indicator of the relative strength of insolation during different observation periods.
7. Several males, including the bird observed most intensively, were color-marked with spots of airplane dope on the back; each individual was given a unique color combination; see also L. L. Wolf and F. G. Stiles, *Evolution* **24**, 776 (1970).
8. I was unable to follow a territorial bird at *Nicotiana* for a full day because territoriality broke down at dawn and dusk as a result of an influx of female and immature *C. anna* into feeding areas at these times.
9. Pearson (*1*) obtained perching metabolism at different temperatures by linear interpolation between metabolic values recorded at 12° and 24°C. The slope of the line joining these two points is very similar to the value for thermal conductance of *C. anna* obtained by R. C. Lasiewski [*Physiol. Zool.* **36**, 124 (1963)]. Hence, I felt justified in continuing this type of measurement to obtain perching metab-

olism for temperatures beyond this range. I assume that variations in perching metabolism due to song, preening, and other activities are negligible, at least relative to the overall metabolic differences between perching and flight.

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Identification of Each Human Chromosome with a Modified Giemsa Stain

Abstract. *Differential staining of human chromosomes can be obtained when the pH of Giemsa stain is changed to 9.0 from the usual 6.8. Such staining permits identification of all homolog pairs and distinct regions within chromosome arms. In most instances, the pattern is quite similar to that obtained with quinacrine mustard fluorescence staining. Certain regions, such as the paracentric constrictions in chromosomes A1 and C9, and the distal end of the long arm of the Y chromosome stain differently with the Giemsa 9 technique. The technique is considerably simpler than the quinacrine mustard fluorescence technique and identification of homologs is also easier than in cells stained by the latter.*

The characterization of human chromosomes has been greatly improved by two recently described techniques. The quinacrine mustard (QM) fluorescence technique described by Caspersson *et al.* (*1*) permits the identification of autosomal homologs and the sex chromosomes. The second technique, differential staining of heterochromatic areas after treatment with NaOH, ribonuclease, and standard saline citrate, permits the identification of regions with repetitious DNA as well as the recognition of certain homologs (*2*). We now report a simple modification of the Giemsa stain which produces a banding pattern very similar to that observed with QM fluorescence staining; it also stains certain heterochromatic areas differentially.

A banding pattern similar to that seen with QM fluorescence staining or differential staining of the centromere regions of certain human chromosomes was occasionally observed in our laboratory with routine orcein or Giemsa staining. A systematic study of certain of the variables involved in the Giemsa staining procedure was therefore undertaken in order to develop a more regularly informative staining technique. Cells were cultured for 68 to 70 hours in a complete McCoy's 5A medium with 15 percent fetal calf serum, harvested by treatment with hypotonic KCL (0.075 mole/liter), fixed in a mixture of methanol and acetic acid (3 : 1), spread, and air-dried by blowing. Several aspects of the Giemsa staining procedure were studied in detail. The *p*H of the Na_2HPO_4 buffer and stain was varied from *p*H 5.0 to 12.0 by the addition of citric acid or sodium hydroxide to the buffer. Two milliliters of stain and 2 ml of buffer solution were then added to 96 ml of water. The *p*H was determined with a Beckman Zeromatic *p*H meter. No consistent banding pattern was noted below *p*H 9.0; apparent chromosomal damage was induced above *p*H 10.0, and less clear and less consistent banding patterns were observed. The duration of staining in Giemsa at *p*H 9.0 also proved to be important. When the slides were stained for 1 to 2 minutes, the predominant staining was in the centromere regions; occasional staining of the secondary constriction regions of A1 and E16 was also observed (*3*). When the slides were stained for 4 to 10 minutes, a reproducible banding pattern similar to that seen with QM

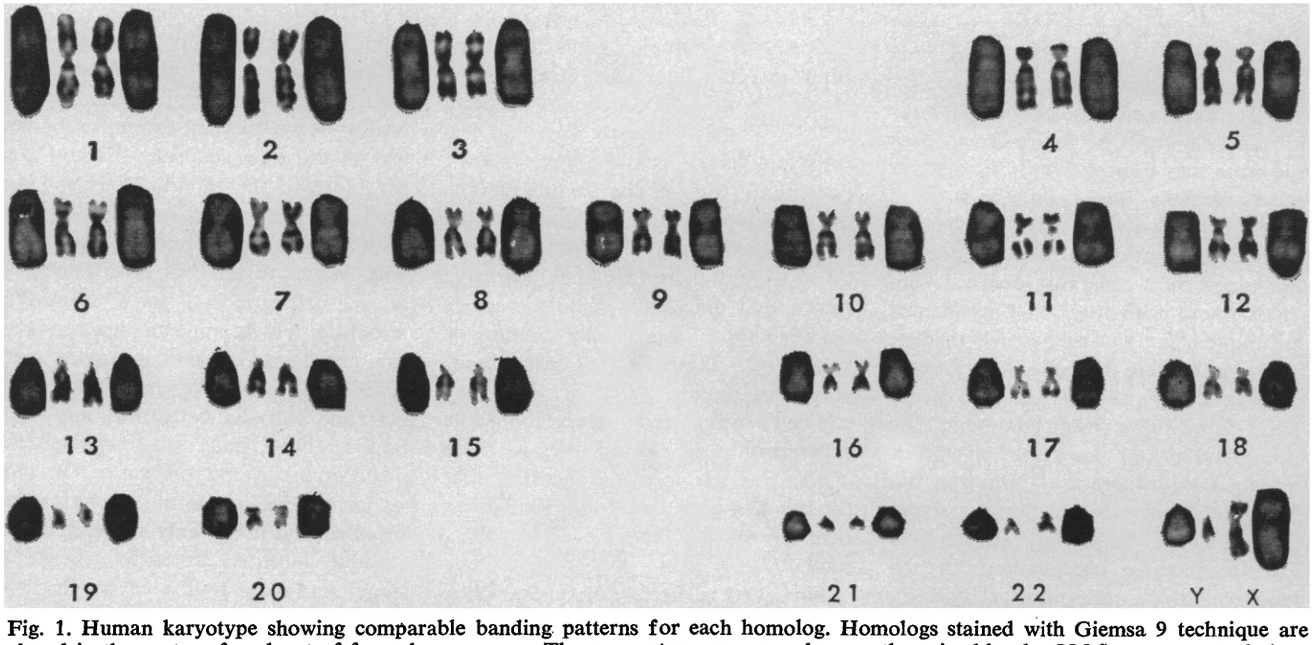

Fig. 1. Human karyotype showing comparable banding patterns for each homolog. Homologs stained with Giemsa 9 technique are placed in the center of each set of four chromosomes. The same chromosomes subsequently stained by the QM fluorescence technique are placed adjacent to these. The comparable banding patterns for homologs and for both techniques are evident.