Technical Report No. 61

THRESHOLD MODEL OF FEEDING TERRITORIALITY:

A TEST WITH AN HAWAIIAN HONEYCREEPER

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ABSTRACT

A cost-benefit model predicting threshold requirements for establishment of feeding territories in nectarivorous birds was tested by comparing 24-hour energy production of nectar with energy budgets in territorial and nonterritorial Hawaiian honeycreepers. The test was positive and demonstrated that nectar productivity was more important in determining establishment of territories than intrusion pressure and floral dispersion.

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INTRODUCTION

Since the natural world appears to be generally in a state of balance with regard to production and utilization of energy, a profitable area of ecological investigation should be the assessment of energetic costs and benefits. However, the mechanisms of natural balances and the relative importances of the parameters that determine these balances are usually difficult to ascertain. The use of quantitative models in such problems can aid clarification. The study of territoriality has been characterized by a lack of tests of theoretical predictions, and this lack recently has become quite apparent (Brown and Orians 1970). In this study we have applied a model to the economics of feeding territoriality in birds. The model has helped elucidate the factors that determine the presence or absence of territoriality in a nectar-eating passerine bird and has enabled us to quantify the importance of each factor. In this paper we define territory in the sense of previous workers (Wolf 1970) as an area "within which the resident controls or restricts use of one or more environmental resources."

Brown (1964) suggested some of the factors that should determine whether feeding territoriality in birds, involving active defense and chasing, is economically feasible. Assuming that energy is potentially limiting, if one or a combination of several factors becomes adequately favorable, then the benefit of territoriality should exceed the cost, a threshold should be crossed, and the establishment of a territory should be favored. Various observations on flower-feeding hummingbirds (Carpenter 1972 and in review, Stiles 1973, Stiles and Wolf 1970, and Wolf 1969) suggested the importance of the following parameters in territorial establishment: the productivity of the food source (nectar), the number of individuals competing for the resource, the dispersion of the flowers supplying the resource, dispersion of advertisement perches, body size, and foraging technique. Hummingbirds are particularly suited to the study of territorial energetics because they are conspicuous and largely dependent on nectar, the energy content of which is easily measured. The basics of the following model were developed (Carpenter in review) from observations (Carpenter 1972) on hummingbird behavior. It has been modified slightly herein to allow energetic descriptions and predictions of the relative importances of cost-benefit parameters for nectar feeding birds in general:

T = Benefit - Cost

where T = calories/time (when T is greater than a certain threshold value the bird should be territorial)

Benefit = (fn) - z

where f = # flowers in territory

    n = cals. of nectar secreted/(flower x time)

    z = cals. of nectar lost to nectar thieves

$$Cost = M + F + R + ci + k_f d_f + k_p d_p$$

where M = maintenance energy of the bird in cals./time
        (energy spent while at rest)

    F = energy spent while foraging at resource, cals./time

    R = energy spent flying between foraging area and roosting area
        twice a day

    c = cals. spent in territorial chases/intrusion

    i = # intrusions/time

    k_f = cals. spent in foraging flights/(meter x time)

    d_f = mean distance between flowers in meters

    k_p = cals. spent patrolling and displaying/(meter x time)

    d_p = mean distance between advertisement perches in meters.

Thus,

$$T = (fn - z) - (M + F + R + ci + k_f d_f + k_p d_p).$$

The model predicts that if $B \geq C$, a bird will be territorial, but if $B < C$ it will not. Conversely, if a bird is territorial, then B must at least equal C, but if it is not, B must be less than C. The simplest way to disprove the model is to show that T of nonterritorial birds is not statistically less than T of territorial birds.

The following is to our knowledge the first attempt to quantify the major 24-hour cost-benefit components that are likely to determine feeding territoriality in a nectarivorous bird.

MATERIALS AND METHODS

The study subject is one of the native honeycreepers on the island of Hawaii, the Iiwi (Vestiaria coccinea, Drepanididae). During the nonbreeding season Iiwi feed primarily upon the nectar of one native flowering tree, Metrosideros collina (Myrtaceae) (Baldwin 1953, Perkins 1913, MacMillen and Carpenter in prep.). This species is brightly color-monomorphic and defends feeding territories among the flowering trees (MacMillen and Carpenter in prep.). Honeycreepers possess the same advantages for study as do hummingbirds; furthermore, they are larger and more sedentary than hummingbirds, and therefore much easier to observe. While territorial they feed primarily on one plant species such that energy input from other species does not complicate the system.

The Iiwi also takes insects (Baldwin 1953) and at times some individuals

become almost completely insectivorous (pers. obs.). This situation is similar to
that in hummingbirds (Carpenter 1972 and in review, Wolf 1970). During the times
that hummingbirds are primarily insectivorous, they do not defend feeding terri-
tories (Stiles 1973, Wolf 1970), presumably because insects are less predictable
in time and space than are flowers (Stiles 1973; see also Brown and Orians 1970).
As in hummingbirds, the Iiwi also showed feeding territorality only when it was
primarily nectarivorous, that is, when almost all of its foraging was conducted at
flowers. The model assumes nectar is the only contributor to B.

Two other honeycreeper species compete in our study area for nectar with the
Iiwi--the Apapane (Himatione sanguinea) and the Amakihi (Loxops virens); the Iiwi
excludes both these species from its territories (MacMillen and Carpenter, in prep.).
Our study area was the Keauhou Ranch on the volcanic slopes of Mauna Loa between
1372 and 1829 m elevation. Study sites were chosen in relatively undisturbed
forest consisting primarily of M. collina and another native tree, Acacia koa. The
forest canopy was about 16m above ground level. Our study was conducted in August
1974 during the nonbreeding season of the honeycreepers.

We selected six mature individuals for study. An individual was considered
nonterritorial if it ignored other honeycreepers feeding on flowers in its foraging
area, and territorial if it successfully chased invaders from its foraging area.
Nonterritorial adult individuals were difficult to locate and to observe, only one
being found in an area that permitted detailed and prolonged observation. The
remaining five individuals varied in the proportion of invaders that they were able
to exclude. We quantified intensity of territoriality by assuming that intensity
is directly related to effort spent on defending the territory and therefore should
be directly related to the calories spent in territorial chases. However, defense
consists also of visual and vocal advertisement to neighbors and intruders, and
this is more effective in keeping out intruders when a territory is small, fewer
chases being necessary on a small territory than on a large one. Thus, the size of
the territory directly affects the calories spent on chases. The most direct way
to correct for this effect of size was to divide the calories by the longest linear
dimension of the territory, which would be the distance vocal advertisement would
have to carry or visual cues be seen in order to discourage a potential invader on
the far edge of the territory. The units of the index are "calories spent on
territorial chases per hour of observation time per meter of territory length or
height."

Each individual bird was observed with binoculars for 8 to 40 consecutive 15-minute periods within a one to four day period: the allocation of time to each activity comprising the cost C for each individual was measured with a stopwatch (after Pearson 1954) and recorded on tape recorders; and environmental temperature was measured in the shade every hour with a Schultheis thermometer. We also measured the dimensions of the foraging area or territory; and we estimated the calories of nectar produced on each foraging area or territory by counting flowers and measuring nectar secretion rates. Techniques of nectar determination are described in Carpenter and MacMillen (1973). Later, the time allocations were translated into energy allocations.

Time at rest during the day consisted of perching and preening. The clocktime of arrival on foraging area in the morning and of departure to a common roost area (MacMillen and Carpenter, in prep.) in the evening and the general location of the roost area were known; speed of flight to the roost area was estimated over known distances with a stopwatch (21 km/hr). This enabled calculation of time spent in flight to and from the roost and thus total time roosting.

In another study (MacMillen 1974) metabolism at different ambient temperatures had been measured during the day in darkness; resting metabolism in the wild at night at known environmental temperatures was calculated from this (Aschoff and Pohl 1970). Daytime resting metabolism in the light is higher than in the dark in the day by a factor of approximately 1.35 (Aschoff and Pohl 1970, Carpenter 1972 and in review, MacMillen and Trost 1967) and this calculation was applied to the day resting time. Maintenance energy (M) was computed by converting metabolism during the night rest and day rest times to calories at each environmental temperature, and summing them over a 24-hour day, which consisted of 13 hours of light.

Nectarivorous honeycreepers forage by flying or vigorously hopping from flower to flower within a dense clump and perching at each flower several seconds to extract nectar, then traveling to another clump with a flight of longer duration. Iiwis occasionally left their territories and gleaned the branches of <u>Acacia koa</u> for insects: these insect foraging areas were not defended. For calculation of energy spent foraging (F) and $k_f d_f$, we distinguished between 1) short flights or hops between nearby flowers or branches (part of foraging at flowers, or at branches while gleaning for insects--F_f and F_{in}, respectively), and 2) longer foraging flights of 1 sec or more between flower clumps (used to calculate k_f), the duration and number of which increase with increasing foraging area (d_f).

To obtain $k_f d_f$ we estimated the velocity of the longer foraging flights by timing flights along flight paths of known length; this speed was 14.8 km/hr. By counting total seconds of foraging flights which were 1 second or longer in each time period, and knowing the flight speed in m/sec, the cost of foraging flights ($k_f d_f$) could be approximated from Tucker's (1975) equation (2). The cost of short flights is only approximated, as the equation is most appropriate for long distance flights. However, it is the most recent and accurate flight equation available that enables use of measured flight velocities at known elevations. To obtain F, the relative proportions of hopping-flying and perching in a clump of flowers or on a branch gleaning were stopwatch estimated, the total time foraging in clumps and on branches measured, this total time then separated into flight and rest times, and the appropriate energetic costs applied as for $k_f d_f$ and M, respectively. Total foraging cost equalled $F_f + F_{in}$. In the territorial birds $F_f >> F_{in}$, whereas in the nonterritorial bird $F_{in} >> F_f$.

Territorial Iiwis do not advertise in the same obvious manner as do hummingbirds, but instead patrol their territories and call simultaneously with their foraging. Thus, if a potential intruder is near one edge of the territory, the Iiwi will fly to that part of the territory and forage, increasing both its calling frequency and the proportion of flight-hops to perching while foraging, apparently to become more visually obvious. Thus, advertisement is incorporated in F and $k_f d_f$, and $k_p d_p = 0$.

The time Iiwis spend chasing intruders is constant for each intruder, a 1- or 2-second chase being effective in removing another honeycreeper. Most intruders were Apapane and Amakihi, which are nonterritorial and easily excluded (MacMillen and Carpenter in prep.). The simplest way to obtain the equivalent of ci was to count the total seconds spent chasing in each 15-minute period and apply Tucker's (1975) equation assuming the average flight speed of several timed territorial flights.

The energy expended in flight to and from the common roosting area increases with the distance of the territory from the roost area; these distances were estimated on a U.S.G.S. topographic map and used to calculate (Tucker 1975) flight cost at a flight speed of 21 km/hr.

Energetic calculations assumed 5 cals/$_{cc}$$O_2$ (respiratory quotient of nectar = 1.0) in the nectarivorous territorial birds and 4.8 cals/$_{cc}$$O_2$ in the partly insectivorous nonterritorial bird, since respiratory quotient (RQ) of mixed protein

is about 0.81 (Brody 1964). The nonterritorial bird fed regularly at its flowers, but flower foraging comprised a very small proportion of the total foraging time. The results are robust with respect to the assumptions of RQ.

The rate of nectar production by trees on Iiwi territories was surprisingly consistent ($\bar{x}$ = 0.259 kcals/ inflorescence/24 hr, S.D. = 0.01 kcals/day, N = 3 trees and 18 flowers) and was assumed to be constant. Some nectar was taken by other honeycreepers intruding while the territorial owners were temporarily out of the area or were not thoroughly defending their territories. The amount of nectar taken by these avian "nectar thieves" was assumed to be directly related to the number of "successful" intruders and to the nectar production on the foraging area. A successful intruder was able to remain on the territory or foraging area about 3 min; unsuccessful intruders were almost immediately removed either by chase or by display. Thief-minutes per day were calculated (assuming an average visitation time of 3 minutes per thief) and multiplied by the nectar production in kcals/min to give kilocalories lost to thieves per day for each foraging area. Since a four-person team was available and tape recorders used to record data, information was gathered efficiently and simultaneously under the same climatic conditions. Approximately 200 person-hours were spent gathering data for this study.

RESULTS

Table 1 shows the results with the total energy budget of each individual broken into the percentages that each factor contributes. The T value of the nonterritorial bird was significantly lower than the mean T of the territorial birds (one sample t-test .01 < p < .025), thus supporting the model.

DISCUSSION

The values for T are all much greater than 0 in all territorial birds regardless of territorial intensity. Some nectar is taken by insects, but up to 9 kcals remain unused on the territories. This suggests that in order to establish a territory, an Iiwi must have available not only enough nectar to satisfy its basic energy requirements but also a certain margin of excess, perhaps to enable it to maintain a territory for a longer time as flowering on its territory declines. Perhaps also the excess acts as an energy store that can be drawn upon during

TABLE 1. Energy available on the foraging area and energy spent by $\underline{V}$. $\underline{coccinea}$.

Bird	Longest linear dim. of area (m)	Terr. index	f	n (kcal/infl/24hr)	z (kcal/area/24hr)	B	M	F	R (kcal/bird/24hr)	ci	$k_f d_f$	C	T
XV	13.3	2.03	115.5*	.259	1.38	28.53	4.84	12.40	.53	.35	.23	18.35	10.18
							26.4%	67.6%	2.9%	1.9%	1.2%		
XIII	3.3	1.61	128	.259	3.51	29.64	4.70	10.10	.53	.07	.18	15.58	14.06
							30.2%	64.8%	3.4%	0.4%	1.2%		
near XV	15.7	0.69	249	.259	25.50	38.99	4.66	9.65	.53	.12	.19	15.15	23.84
							30.7%	63.7%	3.5%	0.8%	1.3%		
17B	41.7	0.13	80	.259	0.44	20.28	4.65	9.50	.48	.06	.41	15.10	5.18
							30.8%	62.9%	3.2%	0.4%	2.7%		
17A	37.3	0.02	120	.259	0.44	30.64	4.70	9.59	.48	.01	.32	15.10	15.54
							31.1%	63.5%	3.2%	0.1%	2.1%		
0	67	0.00	37	.259	7.185	2.40	4.65	7.49	.81	0	.41	13.36	-10.96
							34.8%	56.0%	6.1%	0.0%	3.1%		

* average of 2 counts made 1 week apart

stressful times, such as inclement weather that occurs frequently at these eleva-
tions and that would raise maintenance energy (M) and energy spent foraging (F).
The results of an enrichment experiment (MacMillen and Carpenter, in prep.) were
consistent with these ideas: for three days we enriched XV's territory by periodi-
cally refilling flowers with a 20% sugar solution, expecting the bird to shrink
its territory in response to approximately a doubling of energy available.
Although foraging time was drastically reduced, the bird continued to defend its
original territorial boundaries, and hence was protective of even a greater energy
surplus. Previous workers (Brown 1964, Brown and Orians 1970) have suggested that
a guaranteed food supply over a length of time may be a "goal" of territoriality.

T values in the less intensely territorial individuals are probably more
consistent than indicated in Table 1. The individual with an index of 0.69 had a
high T caused by an unusually high number of flowers. Our observations were made
during the first day that it was setting up its territory--the territory probably
later shrank in size and number of flowers. The individual with an index of 0.13
had an unusually low number of flowers but it also seemed to have another foraging
area out of our vision. The only intermediately territorial bird that was known
to have an established territory of at least several days, and whose territory was
completely observable (17A), had a T value similar to that of the two more highly
territorial individuals.

The cost C declines with decreasing intensity of territoriality. As the
intensity of territoriality increases, the % resting component of cost C decreases
because of active defense (c) and advertisement (incorporated into F and k_f),
concomitant increase in energy expended, and the resultant need to increase
foraging time and therefore F and k_f. The cost of territorial chasing was sur-
prisingly low, from 0.1 to 1.9% of the 24-hour energy budget, C, and from 0.1 to
2.7% of the daytime energy budget. In two cases (17A and 17B) this was because the
area had low densities of honeycreepers and thus few invaders. Even when honey-
creeper densities were high (XV, XIII, "near XV"), calories used in territorial
chase (ci) was low because of two factors: 1) vocal and visual advertisement is
very effective on small territories (compare ci in XV with that in the equally
effectively territorial XIII, whose territory was nearby but much smaller, therefore
suffering less intrusion); and 2) invaders of all species were usually easily
discouraged by a single brief chase and were not as persistent nor as persistently
chased as are, for example, hummingbirds. In hummingbirds, active defense comprises

3.4% of the nonbreeding season daytime energy budget (Pearson 1954) and 12-16% of the breeding season daytime energy budget (Stiles 1971).

Size of foraging area affects $k_f d_f$, of course. This can be seen in comparisons of individuals with similar territorial intensities but different-sized territories, such as XV compared with XIII, and 17B with "near XV".

It should be apparent from the data in Table 1 that the single most important factor in determining territoriality in the Iiwi is the number of flowers (f) within the foraging area. That the flower number is generally constant for territorial Iiwis is supported by two observations made for another study (MacMillen and Carpenter, in prep.). In one area that had several Iiwis, the territories of one highly territorial and one intermediately territorial Iiwi were observed, and five other honeycreeper foraging areas were assessed for their numbers of blossoms. The blossom counts (f) on the two territories were 140 and 121, while the counts on the other five areas, which possessed no territorial Iiwis, were: 109, 92, 66, 32, and 18. Furthermore, nine days later we returned and found that the territory that had possessed 121 flowers now possessed only 83 and had been abandoned. It is obvious that n (calories of nectar secreted/flower x time) is equally important as f, since an equal percent change in either f or n would have an identical effect on B. It may not be accidental that n of trees on Iiwi territories was so consistent; n varies more among randomly chosen $\underline{M}$. collina (Carpenter, in prep.).

On the other hand the birds seemed flexible in the degree of flower dispersion that could be tolerated within the territory, as the longest linear dimension of territories ranged from 3.3m in bird XIII to 41.7m in bird 17B. This is reasonable when one sees the effect of distance (d) on the parameters in the territorial equation: d affects only ci and $k_f d_f$, two of the three compartments that contribute the least to C in honeycreepers. The effect of d may be more important in hummingbirds if the calories used in territorial chases (c) is indeed relatively greater (Pearson 1954, Stiles 1971).

The only other factor that could be critical for the feasibility of establishment of territory by Iiwis was the number of intrusions. This has a double effect by contributing both to z and to ci. In order to quantify the relative importances of f, n, d, and i, we halved each of those parameters one at a time to see the effect on T for each individual. Halving f or n reduced T by 82-196%. Halving the number of intrusions increased T by 1.4-54%. Halving d increased T by 0.7-4.5%. On the average nectar production (f or n) was 8 times more important than

intrusions (i) in determining territoriality, and intrusions (i) in turn were 8 times more important than distance between flowers (d). Intrusions should be relatively more important in birds with larger c, such as hummingbirds.

CONCLUSION

This paper has shown that by construction of a simple quantitative model and by a careful accounting of energy production and allocation, it is possible to separate the various parameters that affect the territorial behavior of birds and actually to quantify their relative importances. Such a technique could prove to be a powerful tool in the analysis of animal behavior in general, for it allows detailed quantification, reflected in terms of energetic costs and benefits, of each of the major components comprising the overall behavior.

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