

Age, Coloration and Dominance in Nonbreeding Hummingbirds: A Test of the Asymmetry Hypothesis

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Summary. During the nonbreeding season, adult Anna and black-chinned hummingbirds (*Calypte anna* and *Archilochus alexandri*) have lower defense costs and more exclusive territories than juveniles. Adult *C. anna* are victorious over juveniles in aggressive encounters, and tend to monopolize the most temporally predictable resources.

Juveniles are more successful than adults at stealing food from territories (the primary alternative to territoriality), presumably because juveniles are less brightly colored. Juveniles have lighter wing disc loading than adults, and consequently should have lower rates of energy expenditure during flight. Reduced flight expenditures may be more important for juveniles because their foraging strategy requires large amounts of flight time. These results support the contention of the asymmetry hypothesis that dominance can result from a contested resource being more valuable to one contestant than to the other.

Among juveniles, defence costs are also negatively correlated with age and coloration; amount of conspicuous coloration is negatively correlated with the number of bill striations, an inverse measure of age.

Introduction

Although behavioral dominance is one of the most pervasive concepts throughout studies of social behavior, explanations of the ultimate causes of dominance remain in a preliminary theoretical stage. One well-developed hypothesis proposes that dominance results from an asymmetry between contestants in their expected net gain in inclusive fitness from exert-

ing dominance – a contestant with a given expected net benefit from victory should be dominant to one with a lower expected net benefit (Parker 1974; Maynard Smith and Parker 1976; Popp and DeVore 1978). According to this hypothesis, net benefits from fighting for and controlling contested resources include a variety of components: gains and losses of resources, abilities to inflict and avoid injury, degrees of genetic relatedness between contestants, and alternatives available to contestants.

Past studies have analyzed these components to varying degrees. Correlations between body size and dominance are ubiquitous in the literature, larger body size presumably conferring dominance by increasing a contestants ability to inflict injury or withstand attacks (reviewed by Wilson 1975). Experimental investigations support other aspects of the asymmetry hypothesis: in butterflies (*Pararge aegeria*) territorial ownership confers dominance (Davies 1978) and in toads (*Bufo bufo*) low croak pitch (which is associated with large body size and dominance deters opponents (Davies and Halliday 1978).

A principal untested aspect of the asymmetry hypothesis states that dominance can result from differences between contestants in their expected net gain from the contested resource. A logical first step in testing the validity of this contention is to determine whether dominant individuals obtain a greater net gain than subordinates from controlling contested resources. The present study tests this prediction, focusing on dominance relations between adult and juvenile hummingbirds competing for control of feeding territories.

In most social systems, adults are dominant to juveniles (Wilson 1975). Although dominance by adults in contests over territorial ownership has been documented in birds (Watson 1967; Krebs 1971), the determinants of this dominance are not well understood (Davies 1978). This problem is especially intri-

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guing because adult birds do not have the substantially increased body sizes, relative to juveniles, that commonly occur in other taxa (presumably, body sizes of adults and juveniles are similar because constraints of flight restrict suitable ranges of body sizes relative to wing areas; Mayr 1963).

We conducted our experiments on male Anna and black-chinned hummingbirds (*Calypte anna* and *Archilochus alexandri*) during the nonbreeding season (July through November). At this time of year, measurements of asymmetries is simplified because costs and benefits of territorial behavior seem to result primarily from energy expenditure and gain (Ewald and Carpenter 1978). Degrees of relatedness between interacting individuals are probably extremely low because of high rates of immigration to and emigration from local areas, with migrants traveling individually.

Our specific prediction was as follows: If adults are dominant to juveniles in contests over monopolization of food, then the measured net gain from aggressive control of the food source should be greater for adults than for juveniles. We gathered data on what we believe to be the three most important components of this net gain: costs of defense, degree of resource monopolization and the value of the contested resource relative to alternatives.

Materials and Methods

Observations were made over five years of study at the Tucker Wildlife Sanctuary, Santa Ana Mountains, California. When morphological characteristics were insufficient for identifying individuals, birds were marked by an airborne-marking method (Fig. 1) or by spreading a paste of Rhodamine B dye and vegetable oil on a perch in front of a feeder. Birds were weighed while feeding at feeders using an aluminum perch suspended from a Pesola 5-g scale, modified to measure weights above 5 g (Fig. 2). The weights at the beginning and end of at least one feeding were averaged to estimate the mean weight for each bird.

Measurements of wing length and coloration were made on specimens from the Museum of Vertebrate Zoology, University of California, Berkeley, and the Washington State Museum, University of Washington. Wing lengths were measured only on unworn wings; if both wings were unworn, we assigned the mean of the two lengths to that specimen. Amounts of iridescent coloration on throats and crowns were measured by using transparent acetate squares (1, 4, and 10 mm²) mounted on cardboard pointers.

Our study site had a highly predictable feeding area in which sucrose solution 20%–30% (by weight) was supplied continuously at an unrestricted rate throughout the study and several years prior to the study. In an adjacent area (20–250 m away) no food was provided for several months prior to each field season. At the beginning of each field season, feeders identical to those on the highly predictable area were placed on this less predictable area for variable lengths of time greater than one day. Uncertainty (sensu Colwell 1974) on a day-to-day time scale is relevant because hummingbirds use up to two weeks of prior information about

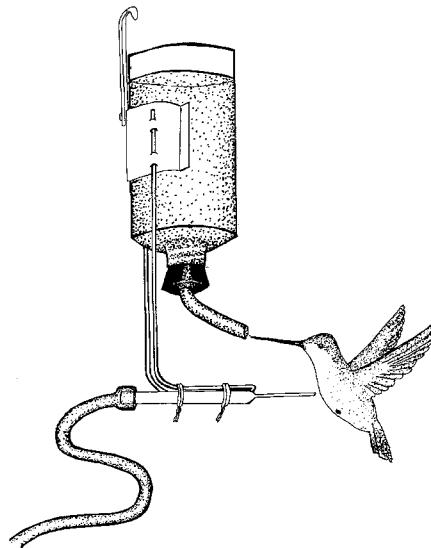


Fig. 1. Airborne-marking method. A capillary pipette was attached to a bendable but rigid metal wire (2 mm in diameter) by using paper-covered wire. When birds came to feed, coloring agent (thinned paint or enamel, or a solution of Rhodamine B and vegetable oil) was ejected by blowing through the free end of the tube

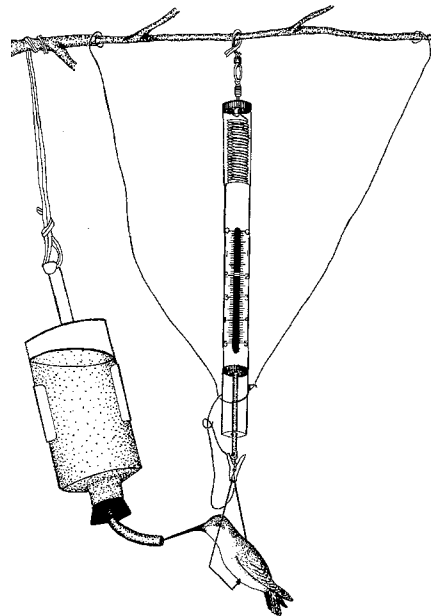


Fig. 2. Perch-weighing scales. Rigid plastic tubing was used to extend the length of the scale so that total weights (perch plus bird) above 5 g could be measured. The weights were read from the scale by using Bushnell 25–45× Spacemaster telescopes mounted on tripods. These readings were converted to actual weights of the birds by using a conversion factor obtained from a Mettler top-loading scale. Aluminum wire (1 mm diameter) stabilized the scale and perch against gusts of wind. These stabilizers did not affect measurements because they were in loose or no contact with the scale during the weighing operation. The area of the perch grasped by the bird was covered with tape to increase its diameter

Table 1. Morphological characteristics and power input for flight. Number of birds in each sample are in parentheses. Wing and weight measurements are followed by standard deviations. The differences in wing length are statistically significant for both *C. anna* and *A. alexandri* ($P < 0.025$ and $P < 0.001$, respectively, one-tailed *t*-test). Wing-loading was calculated from equation 1 in Feinsinger et al. (1979)

Species	Age	Body weight (g)	Wing length (cm)	Wing disc loading (g/cm ²)	Required power for flight (W)	
					Linear flight	Hovering
<i>Calypte anna</i>	Adult	4.72 ± 0.37 (39)	4.89 ± 0.04 (32)	0.0427	0.62	1.26
<i>Calypte anna</i>	Juvenile	4.72 ± 0.43 (21)	4.93 ± 0.07 (21)	0.0418	0.61	1.23
<i>Archilochus alexandri</i>	Adult	3.79 ± 0.11 (4)	4.20 ± 0.08 (30)	0.0456	0.53	1.04
<i>Archilochus alexandri</i>	Juvenile	3.81 ± 0.41 (8)	4.35 ± 0.13 (8)	0.0427	0.52	1.02

resource quality in their decisions to defend feeders (Ewald, to be published). In general, distances between feeders were 3–10 m, each territory containing one feeder but no flowers. In both areas, age classes of owners (male *C. anna*) were recorded during the first two weeks of each field season. Juvenile males were distinguished from females by the presence of crown coloration, announcement song, and smaller amounts of white coloration on their rectrix tips (Williamson 1956)

Time spent in defense by adults and juveniles was compared by simultaneously observing neighboring territories for 1.5-h periods. One territory in each pair of neighbors was owned by an adult, and the other by a juvenile. Each territory contained one feeder providing 0.55 M sucrose solution (20%) at an unrestricted rate. With this experimental design, environmental variables that could affect defense costs (e.g., time of day, energy availability, vegetation structure) were approximately or exactly the same for each owner. All comparisons were made on the less predictable site after each owner had at least one day of ownership. This time scale conforms to the amount of time that is required for new owners to equilibrate on their territories (Copenhaver and Ewald, to be published). Time expenditures were converted to energy expenditures using Montgomery's (1979) equations.

Results

Available data indicate that adult hummingbirds are dominant to juveniles in contests over control of food resources. Stiles (1973) found that adults won 68 of 81 aggressive encounters between adult and juvenile *C. anna* on a feeding area that was not incorporated into territories. Although Stiles did not analyze these data statistically, the trend for adults to be victorious is highly significant ($P < 0.001$, Sign test).

This dominance relationship is also apparent in patterns of territorial ownership. On the highly predictable area 16 of the 18 owners were adults. On the less predictable area, only 26 out of 60 owners were adults ($P < 0.001$, Fisher exact test).

In both *C. anna* and *A. alexandri*, adults and juveniles have virtually identical body weights (Table 1, column 3); thus in comparison to many other systems, effects of body size on this dominance relationship should be relatively unimportant.

Table 2. Costs of territorial defense, feeding rates of owners, and success by intruders. For all rates and percentages, units of time in denominators refer to time that owners were present on territories rather than total observation time. 'Seconds in defense' includes time spent in miscellaneous flight on the territory because this flight may function as territorial advertisement (Ewald and Carpenter 1978; Carpenter and MacMillen 1976). Levels of statistical significance (one-tailed Walsh test; Siegel 1956) and the number of pairs of birds in each sample are given in parentheses. These sample sizes include all pairs for which the relevant data were collected

	<i>Calypte anna</i>		<i>Archilochus alexandri</i>	
	Adult	Juvenile	Adult	Juvenile
Time spent in defense (%)	3.8 ($P=0.027$, 8)	6.8	6.0 ($P=0.016$, 6)	16.0
Joules spent in defense per min	2.15 ($P=0.012$, 8)	3.15	3.45 ($P=0.016$, 6)	7.38
Seconds per chase	4.1 ($0.15 > P > 0.10$, 8)	4.6	2.5 ($P=0.016$, 6)	4.1
Chases per min	0.53 ($P=0.057$, 8)	0.79	1.20 ($P=0.016$, 6)	2.62
Time spent feeding by owners (%)	1.0 ($P=0.047$, 6)	1.3	1.2 ($0.15 > P > 0.10$, 6)	1.4
Seconds feeding by intruders per min	0.004 ($P=0.031$, 6)	0.805	0.080 ($P=0.063$, 6)	0.512

In both species, adults spent less time in defense than juveniles (Table 2, row 1). The extra time spent in defense by juveniles is due to longer chases and higher frequencies of chases (Table 2, rows 3 and 4).

By our estimates of energy expenditure, adults spent less energy in defense than juveniles (Table 2, row 2). To obtain these estimates, linear flight speeds were measured in the field for *C. anna*. Speeds were 7.7 m/s when chasing intruders and 6.0 m/s when returning from chases (28 and 10 measurements, respectively, on two birds; $P < 0.01$, two-tailed *t*-test). From

Table 3. Costs of defense for juveniles possessing different amounts of coloration. Cost indices and notations are the same as in Table 2

	<i>Calypte anna</i>		<i>Archilochus alexandri</i>	
	Bright	Dull	Bright	Dull
Time spent in defense (4)	7.8 ($P=0.024$, 12)	11.3	13.8 ($P=0.023$, 7)	16.7
Joules spent in defense per min	4.05 ($P=0.47$, 12)	5.78	6.59 ($P=0.016$, 7)	7.41

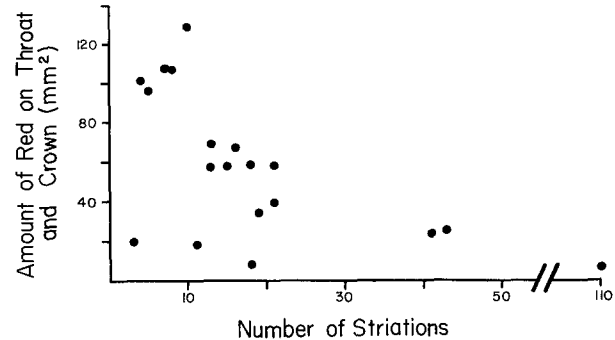
these speeds, mean rate of energy expenditure during chases (Table 1) was estimated to be 1.02 times the energy spent at the speed that minimizes energy spent per unit time. Linear flight costs for *A. alexandri* were also assumed to be 1.02 times the minimum rate of energy expenditure for linear flight.

To check our estimates of energy spent in defense, we computed the amount of time that owners fed at their feeders. If adults spend less energy in defense, they should require less food from the feeder. In accordance with this prediction, adults spent less time feeding in both species (Table 2, row 5); however, the difference is statistically significant only in *C. anna*.

The preceding results show that defence costs are less for adults than for juveniles. To determine whether adult owners maintain more exclusive control over their resources, we measured the amount of time intruders fed in the presence of owners. In both species, intruders were less successful at stealing food from territories owned by adults than from territories owned by juveniles (Table 2, row 6).

Juvenile *C. anna* and *A. alexandri* are highly variable in the amount of iridescent plumage on their crowns and throats. Defense costs of juvenile owners possessing different amounts of iridescent coloration were compared by using the same experimental design employed for comparisons of adults and juveniles. The brighter owner of each pair possessed approximately twice as much bright feathering as the duller owner. The brighter juveniles spent less time and energy in defense (Table 3).

The iridescent feathers on throats and crowns of juvenile males grow during the 6–8 months following fledging but prior to the postjuvencal molt of all feathers in these regions (Bent 1940; Williamson 1956). To determine whether the amount of this coloration is positively correlated with age among juveniles possessing such coloration, we checked for a negative correlation between amount of coloration and

**Fig. 3.** Amount of iridescent color on throat and crown of juvenile male *C. anna* versus the number of bill striations, an inverse measure of age. Data are from all available museum specimens with intact bills. We counted only bill striations greater than 0.02 mm in width, on the upper mandible (excluding depressions of the nares)

number of bill striations; amount of striation is negatively correlated with age (Ortiz-Crespo 1972; Stiles and Wolf 1974). Our measurements confirmed this prediction (Fig. 3, $P < 0.05$, one-tailed Spearman $r_s = -0.51$, $N = 19$). Variation in coloration among juveniles does have a substantial age component.

The points in the lower left corner of Fig. 3 could be either females missexed as males, or juvenile males with developmental schedules different from the norm. To eliminate possible effects of misidentification of females as males, we analyzed all specimens possessing more coloration than the maximum amount among females (i.e., greater than 30 mm of red on crown and throat). These 13 specimens still show a significant negative correlation between amount of red coloration and number of bill striations ($P < 0.01$, $r_s = -0.74$).

At our research site the primary alternative to territorial defense was to intrude on territories. To test for differences in intrusion success between adults and juveniles, observations were made in the same experimental setup that was used to document differences in defense expenditures. When owners were present, none of the 47 observed intrusions by adult males resulted in successful theft of food. In contrast, eight of 63 intrusions by juvenile males were successful ($P = 0.03$, two-tailed Fisher exact test, mean seconds feeding by juveniles per intrusion was 0.5). When owners were absent there was no statistically significant difference between intrusion success of adults and juveniles. Mean seconds feeding per intrusion were 14.4 ± 10.3 ($N = 51$ intrusions) and 14.7 ± 12.1 ($N = 59$), respectively ($P = 0.42$, two-tailed Mann-Whitney U test).

Discussion

Dominance and Asymmetric Net Gains

The results support the contention that dominance can result from an asymmetry between contestants in their expected net gains from contested resources. Adults are dominant to juveniles, have lower defense costs, control resources more exclusively, and have poorer alternatives to territoriality.

The dominance of adults over juveniles is indicated both by Stiles' (1973) observations on neutral feeding areas, and by the tendency for adults to control the most temporally predictable resources. The latter finding was not due to adults having first access to the highly predictable feeders seasonally. To the contrary, juveniles probably had first access to these feeders; the feeders were not incorporated into breeding territories defended by adult males, and many juveniles fledge months before adult males abandon breeding territories to defend the predictable feeders (breeding territoriality of adult male *C. anna* is described by Pitelka [1951]; Williamson [1956]; and Stiles [1973]). Brief observations of these feeders during the latter part of the breeding season (April and May) revealed no long-term ownership. Rather, juveniles and adults fought brief skirmishes near the feeders, generally not defending them for more than a few hours.

We also know that many adults without territories were intruding on territories in the less predictable site; thus, juveniles were not defending territories in the less predictable site simply because all adults in the population already owned territories.

Effects of starvation on dominance have been documented for a variety of animals (Bruce 1941; Hazlett 1966; Nowlis 1941; Wise and Zimmerman 1973). In our experimental system a given quantity of food will not be of different value to contestants because of differences in their levels of starvation; both adults and juveniles can gain their total daily requirements within a few hours of intrusion time (Ewald, to be published). This high level of intrusion success is due to intruders being extremely successful when they encounter a territory in which the owner is absent. Intruding on territories with more restricted productivity (e.g., territories containing flowers) in the owners' absence would be less profitable because owners tend to feed before departing from a territory (Ewald and Carpenter 1978). The artificiality of our system therefore eliminates starvation as a complicating factor, but increases the apparent importance of intruding on territories with absent owners relative to territories with present owners.

Age, Plumage Characteristics, and Social Structure

Occurrences of bright coloration in female hummingbirds (Wolf 1969, 1975) and experimental dulling of other avian species (Lewis 1972; Peek 1972; Smith 1972) suggest that bright coloration aids in territorial defense. Adult *C. anna* and *A. alexandri* have more bright iridescent coloration on their crowns and throats than juveniles; thus, observed differences in defense costs (Tables 2 and 3) could result from differences in coloration as well as experience.

For juveniles, avoidance of predation is one possible compensating advantage of dull coloration. The relative inexperience of juveniles should not only make them more susceptible than adults to predators, but less able to establish and maintain territories. A weakness of this explanation is that predation on nonnesting North American hummingbirds seems to be extremely rare.

This rarity led us to investigate another potential benefit of dull coloration: Dull coloration could increase intrusion success either by making detection of intruders more difficult, or by reducing the aggressiveness of responses by the owners following detection (e.g., dull coloration could communicate that the intruder offers little threat of usurping the territory). In support of this idea, adults were less successful than juveniles at stealing food in the presence of territory owners.

The addition of bright feathers by juveniles prior to the postjuvinal molt is consistent with both predation and intrusion success hypotheses. As juveniles acquire defense skills, their chances of obtaining a territory and their ability to avoid predators should increase; hence the net benefit of bright coloration should increase with age.

Current evidence suggests that differences in foraging techniques between sexes and between species of hummingbirds are correlated with wing disc loading (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Feinsinger et al. 1979; Kodric-Brown and Brown 1978). Theoretically (Feinsinger and Chaplin 1975), light wing loading should be favorable for individuals that fly for large amounts of time to meet their food requirements because light loading yields low energy expenditure per unit time in flight (Epting and Casey 1975). Heavy loading presumably aids in territorial defense by increasing maneuverability (Feinsinger and Chaplin 1975).

The results of this study suggest that juveniles are less likely than adults to own high-quality territories. Instead, their social role should entail a large amount of flying time traveling between territories, intruding on territories and foraging on undefended

food sources. By the reasoning presented above, juveniles should have longer wings than adults (adults and juveniles have virtually identical body weights, Table 1). This prediction is plausible because molt of the longest primaries occurs near the end of the prolonged postjuvenile molt (Williamson 1956). Measurements of museum specimens confirmed this prediction for both *C. anna* and *A. alexandri* (Table 1).

Greater experience, brighter coloration, and heavier wing loading could all contribute to the lower frequency and duration of chases by adults relative to juveniles (Table 2). Bright coloration could decrease the frequency and duration of chases by increasing the visibility of owners; after noticing the presence of an owner, intruders frequently avoid the territory without attempting to steal food. Once a correlation exists between coloration and fighting ability (greater fighting ability being derived from heavier wing loading or greater experience), adult coloration could also deter intruders by signaling ability to defend resources and readiness to engage in escalated fighting (Maynard Smith and Parker 1976; Parker 1974; Popp and DeVore 1978). Alternatively, juveniles may chase intruders more frequently or for greater durations because juvenile owners are not recognized as owners so readily as are adult owners (Copenhaver and Ewald 1980).

In an evolutionary sense the observed differences in color, behavior, and morphology can be viewed as secondary adaptations which benefit older individuals more than younger individuals because greater experience increases chances of obtaining a territory. The existence of such adaptations in older individuals increases the asymmetry between old and young individuals in conflict over control of resources. In contrast, by the reasoning presented above, the differences in survival between adults and juveniles during the nonbreeding season should be less than if both classes had the same color, behavior, and morphology.

The estimates of asymmetry between adults and juveniles in this study are conservative because adults may expend less energy than do juveniles in fights over territorial ownership and they also may be more able to inflict and avoid injury. To test the asymmetry hypothesis more thoroughly, such variables need to be quantified, and asymmetries in values of contested resources need to be reversed sufficiently to determine whether dominance relationships can be reserved.

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