

GREATER FOOD AVAILABILITY REDUCES TARSUS ASYMMETRY IN NESTLING BLUE TITS

FABRIZIO GRIECO¹

Netherlands Institute of Ecology, Centre for Terrestrial Ecology, P.O. Box 40,
NL 6666 GA Heteren, Netherlands

Abstract. Previous work has shown that the quantity or quality of food affects the degree of asymmetry in bilateral body traits in adult birds, but so far there is no evidence that this is the case in early phases of growth too. I studied asymmetry of tarsus length of nestling Blue Tits (*Parus caeruleus*) in relation to supplemental feeding. I offered food, in the form of mealworms (*Tenebrio molitor*) and wax moth (*Galleria mellonella*) larvae, to the adults during the brood-rearing period. The parents consumed the extra food themselves and fed the brood an amount corresponding to one-third of the brood's total food intake. Food supplementation resulted in reduced asymmetry of nestling tarsus length, indicating that body asymmetry in early phases of life, not only in adult birds, depends on energy or protein intake.

Key words: breeding, developmental stability, *Parus caeruleus*, supplemental feeding experiment, symmetry.

Mayor Disponibilidad de Alimento Reduce la Asimetría del Tarso en Polluelos de *Parus caeruleus*

Resumen. Investigaciones previas han demostrado que la cantidad o calidad de alimento disponible afecta al grado de asimetría bilateral de rasgos corporales en aves adultas, pero hasta ahora no se ha demostrado si este proceso también sucede en las fases tempranas del crecimiento. En este estudio investigué la asimetría de la longitud del tarso en polluelos de *Parus caeruleus* con relación a la administración de una dieta suplementaria. Se ofreció alimento a los adultos durante el periodo de cría en forma de larvas de escarabajo de la harina y larvas de polilla de la cera. Los padres consumieron el alimento adicional y entregaron una cantidad correspondiente a un tercio de la ingesta total de alimento de los polluelos. El suplemento de alimento resultó en una reducción significativa en la asimetría de la longitud del tarso de los polluelos, indicando que el estrés ambiental mediado por el comportamiento de aprovisionamiento efectuado por los padres afecta a la

asimetría del desarrollo corporal en fases tempranas de la vida.

In birds, bilateral traits like tarsi and flight feathers are expected to be identical in size on the two sides (left and right), as they are assumed to be under control of the same genome and environment. However, this symmetry is rarely the case. Bilateral structures have been found to be more or less asymmetrical because of environmental (Hoffmann and Parsons 1991, Parsons 1992) or genetic stress (Palmer and Strobeck 1986, Leary and Allendorf 1989, Parsons 1990, 1992). Fluctuating asymmetry (Ludwig 1932, van Valen 1962, Palmer and Strobeck 1986) refers to small, random deviations from perfect symmetry of bilateral traits and is assumed to be a measure of the ability of an organism to develop bilateral characters identically (developmental stability; Zakharov 1992). Most studies on the effects of environmental stress on fluctuating asymmetry are correlative, and, among the experimental ones, very few have investigated the effect of food (with the exception of some studies on insects; Bjorksten et al. 2000). In birds, food availability is known to affect feather asymmetry in adults (Swaddle and Witter 1994, Nilsson 1994); however, it is still unclear whether that is the case for birds in early phases of life, especially in natural conditions. In a recent book on growth in birds (Starck and Ricklefs 1998), the terms "asymmetry" and "fluctuating asymmetry" do not even appear in the subject index. Hovorka and Robertson (2000) found no evidence for an effect of food deprivation on body asymmetry of nestling Tree Swallows (*Tachycineta bicolor*). It is clear that we need more studies that investigate the mechanisms that give rise to developmental instability, particularly by manipulating behaviorally mediated environmental stress.

In this study, I examine the effects of food availability on the asymmetry of tarsi in nestling Blue Tits (*Parus caeruleus*). The reproductive success of this species depends on the abundance of insect food, primarily caterpillars, which varies markedly during the breeding season (Gibb and Betts 1963, Nur 1984, Perrins 1991). Especially when the adults raise their brood well before or after the peak period of caterpillar abundance, food stress is likely to increase the degree of body asymmetry, because fewer resources are directed to the control of developmental precision. An experimental increase in food availability is predicted

Manuscript received 15 August 2002; accepted 7 April 2003.

¹ Present address: Pomona 418, NL 6708 CR Wageningen, Netherlands. E-mail: fabgrieco@hetnet.nl

to decrease asymmetry of bilateral characters (Nilsson 1994).

To increase food availability to the nestlings, I provided additional food to the adults in the brood-rearing phase. The parents could either give the supplemented food to the nestlings or eat it themselves. In the latter case, the brood could still benefit from the added food, because the parents would allocate more time to food provisioning, resulting in greater rates of food delivery to the nest (Grieco 2002). In the year I did this study, food-supplemented adults brought to the nest 0.06 ± 0.01 (SE) g dry mass nestling⁻¹ hr⁻¹, significantly more than control, unfed adults (0.04 ± 0.01 g nestling⁻¹ hr⁻¹; Grieco 2002). Therefore, nestlings in food-supplemented nests were expected to grow in better conditions, with positive effects on their body symmetry.

METHODS

The study was carried out in 1999 in the National Park "De Hoge Veluwe" (52°1'N, 5°52'E), central Netherlands, in mixed deciduous forest patches provided with nest boxes. The patches grew on poor sandy soil and were dominated by Scots pine (*Pinus sylvestris*), European oak (*Quercus robur*), and birch (*Betula pendula*), with some occurrence of American oak (*Quercus borealis*) and beech (*Fagus sylvatica*; van Balen 1973). The study area contains 400 nest boxes.

SUPPLEMENTAL FEEDING EXPERIMENT

Mealworms (Coleoptera: *Tenebrio molitor*) and larvae of wax moth (Lepidoptera: *Galleria mellonella*) were placed in small feeding trays ($5.5 \times 3.5 \times 4.5$ cm) inside the nest boxes from the date of hatching of the first egg (day 0) to the date of fledging of the young. At early chick ages (day 0 to 6), food consisted of a mixture of the two species; subsequently it was composed of mealworms only. The quantity of food supplied daily corresponded to about one-half of the brood's daily requirement as reported by Gibb and Betts (1963). The variation in this amount across nestling ages was calculated by taking into account that natural food consumption increases linearly with nestling age and then levels off around the middle of the nestling stage (as reported by van Balen 1973 for the Great Tit [*Parus major*]). I calculated several curves of food amount versus nestling age depending on brood size. For a 12-chick brood, the food amount offered increased approximately linearly from day 0 to day 10, and then leveled off around 20 g day^{-1} . For smaller and larger broods I calculated food amounts proportionally: amount for n -chick brood = (amount of 12-chick brood/12) $\times n$; (more details in Grieco 2002). Feeding trays were replenished each day according to the scheduled amount. Half of the boxes were food supplemented ($n = 11$), while the other half were not and served as controls ($n = 11$). All control nest boxes were at least 50 m from the nearest food-supplemented one, so it is very unlikely that control adults had access to the food added. In addition, video recording at the nest (see below) suggested that control adults never entered food-supplemented nest boxes. Food-supplemented and control boxes were chosen randomly within pairs having similar hatching dates. I assigned different treatment levels to boxes in similar

habitats whenever possible. I classified habitats in wood plots according to the dominant tree species: birch, European oak, mixed European oak and pine, or American oak. Nests of the two treatment groups were represented in those habitats at similar frequencies (number of nests [control:food-supplemented]): birch 1:2, European oak 3:4, mixed 7:4, American oak 0:1; $\chi^2_3 = 2.3$, $P = 0.51$).

For all nests, I videotaped the adults feeding the young. A Sony CCD-TR825E videocamera was placed facing down from the top of the open nestbox. During filming, a wooden box covered the videocamera, while a small lamp placed behind it provided more light in the nest. Nests were filmed twice for 90 min each, the first when the nestlings were 3 to 7 (mean 5.6) days old, the second when they were 9 to 14 (mean 11.5) days old (Grieco 2002). Videotapes were analyzed to assess the rate of consumption of supplemental food.

MORPHOMETRY

I measured left and right tarsi of all nestlings at 10 and 14 days after hatching. Measurements were not blind; that is, at the moment of measurement I was aware of which experimental group the nestling belonged to. Asymmetry was defined as the unsigned difference between the right and the left side (|right - left|). This index included measurement error since I did not take multiple measurements. Thus, it cannot distinguish between measurement error and true fluctuating asymmetry (Swaddle et al. 1994). At both nestling ages, the signed differences (R - L) were distributed normally (Shapiro-Wilk tests, $P > 0.10$), their means did not depart significantly from zero (one-sample t -tests, max. $t_{19} = 0.6$, $P = 0.54$), and were not correlated with trait size within nestling age (correlations, max. $r = -0.2$, $n = 20$, $P = 0.34$). Therefore, no size correction of asymmetry index was applied.

STATISTICAL ANALYSES

I estimated repeatability of tarsus measurements (left and right side) following Lessells and Boag (1987) for the average and Becker (1984) for the standard error. Tarsus asymmetry was analyzed with repeated-measures ANCOVA in Statistica for Windows version 5.5 (StatSoft 1999), where nestling age (expressed in days after hatching) was the repeated-measures factor. Nests were the unit of observations, and average measures per nest were entered in the analysis. Hatching date (expressed as April date, 1 = 1 April, 31 = 1 May), average tarsus length at day 10 and day 14, and brood size at day 10 were entered in the models as covariates, and were excluded if not significant to test for the significance of the effect of food addition. Tarsus length was normally distributed, while unsigned asymmetry was not and therefore was log transformed ($y' = \log(y + 0.5)$).

Of the 22 broods initially studied, one was abandoned by the parents at hatching, and another was unusually small. I excluded these nests from analysis, resulting in 20 total nests (10 in each experimental group). Variables are reported as means \pm SE. Control and food-supplemented broods did not differ in hatching date, tarsus length at day 10 and 14 or brood size (t -tests, max. $t_{18} = 1.7$, $P = 0.12$).

TABLE 1. Repeatability estimates (r) of tarsus length in Blue Tit nestlings for two ages posthatching in food-supplemented and control nests. Repeatability was calculated from a one-way ANOVA with individual as a factor (n = number of nestlings). Tarsus length was entered as deviation from the nest average. Repeatability estimates did not differ between control and food-supplemented nests (t -tests within age classes, max. $t_{130} = -0.22$, $P = 0.17$).

Day	Treatment	n	$r \pm SE$	df	F	P
Day 10						
	Control	67	0.95 ± 0.01	66, 67	39.7	<0.001
	Food-supplemented	65	0.94 ± 0.01	64, 65	33.9	<0.001
Day 14						
	Control	67	0.87 ± 0.03	66, 67	13.9	<0.001
	Food-supplemented	65	0.92 ± 0.02	64, 65	22.9	<0.001

RESULTS

FOOD CONSUMPTION

The parents took all larvae offered daily in 183 (89%) of the 205 nest-feeding days ($n = 10$ food-supplemented nests). When the young approached fledging (17–20 days after hatching), mealworms were found during the check of nestboxes on the subsequent day, suggesting that the amount offered at that stage exceeded the need of the parents and the brood. During videotaping sessions, the adults took on average 21.5 ± 3.5 items hr^{-1} (range 0–49, $n = 20$ videotaping sessions). However, the adults delivered to their young only $35 \pm 7\%$ (range 0–100%, $n = 19$) of the food items taken from the tray. As a result, the broods received 16.3 ± 3.5 ($n = 20$) extra food items hr^{-1} , which corresponded to approximately one-third of the total food amount consumed (estimate: 0.06 ± 0.01 g dry mass nestling $^{-1}$ hr^{-1} ; Grieco 2002).

EFFECTS OF FOOD SUPPLEMENTATION

Tarsus length was highly repeatable, and repeatability did not differ between control and food-supplemented

nests (Table 1), suggesting that the measurement error was similar between nestlings of the two groups.

Food supplementation did not result in greater skeletal size of nestlings before fledging. The tarsi of food-supplemented nestlings were similar in length to those of control nestlings (repeated measures ANCOVA, effect of food addition, $F_{1,18} = 2.3$, $P = 0.15$). However, tarsi of food-supplemented nestlings were more symmetrical than those of control nestlings, both at day 10 and day 14 after hatching (Fig. 1; repeated measures ANCOVA, effect of food addition, $F_{1,18} = 8.9$, $P < 0.01$; food addition \times nestling age interaction, $F_{1,18} = 1.9$, $P = 0.18$). The degree of asymmetry did not change significantly with nestling age ($F_{1,18} = 0.7$, $P = 0.40$); this was also the case when expressing asymmetry relative to trait size). Brood size, tarsus length, and hatching date did not affect tarsus asymmetry (repeated measures ANCOVA, all $P > 0.09$). Thus, food supplementation reduced asymmetry of tarsi in Blue Tit nestlings, independent of their developmental stage.

DISCUSSION

This study provides experimental evidence that asymmetry of tarsi is influenced by the feeding conditions in which nestlings grow. Food-supplemented Blue Tit nestlings had more symmetrical tarsi than controls, both when 10 and 14 days old. In *Parus* species tarsi generally grow until 14–15 days after hatching (O'Connor 1977, van Noordwijk et al. 1988, Kunz 1999), so the effect of food addition on tarsus asymmetry presumably persisted at least until fledging.

With this data set I could not properly estimate measurement error, which complicates the reliability of my measure of fluctuating asymmetry. However, the difference in tarsus asymmetry between the two experimental groups was highly significant, leaving few doubts on the effect of feeding conditions on tarsus asymmetry in nestling Blue Tits. It is possible that the higher degree of asymmetry in unfed control broods was the result of a greater measurement error in this group. However, the estimates of repeatability of tarsus length suggest that the magnitude of the measurement error was similar between control and food-supplemented broods, indicating that the effect of food manipulation was not an artifact.

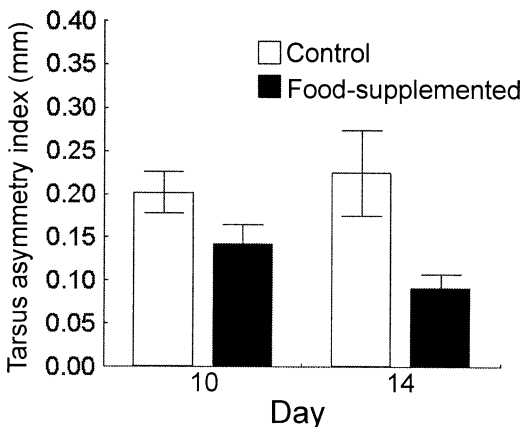


FIGURE 1. Degree of asymmetry of tarsus length of Blue Tit nestlings in control and food-supplemented nests, at 10 and 14 days after hatching. Sample size is 10 nests for each group.

Previous studies have provided contrasting evidence for an effect of food abundance on body asymmetry. Björklund (1996) found that Blue Tit nestlings attended by only the female parent (and that presumably suffered food shortage; Sasvári 1986) had feathers as symmetrical as those in broods attended by two parents. Björklund (1996) concluded that food stress did not influence asymmetry in Blue Tits early in life, although he did not measure asymmetry in other traits. Swaddle and Witter (1994) found that the degree of primary-feather asymmetry in adult European Starlings (*Sturnus vulgaris*) was negatively correlated with an index of fat reserve, providing an indication that energetic stress plays a direct role in the development of asymmetry. The results of my study indicate that the quality or quantity of food affects the degree of body asymmetry in young birds too. More importantly, they show that environmental stress mediated by parental behavior influences asymmetry of a trait (tarsus length) that is likely to persist during life, and may have fitness consequences.

I failed to find an effect of nestling age on tarsus asymmetry. Nestlings in both experimental groups showed the same degree of asymmetry at day 10 and at day 14, when growth is assumed to be at its maximum. This contrasts with many empirical studies where asymmetry of certain traits decreases at the end of their development (Teather 1996, Møller and Swaddle 1997, Swaddle and Witter 1997, Aparicio 1998, 2001), while other studies including those on bone growth have found increasing asymmetry with ontogeny (Chippindale and Palmer 1993, Hallgrímsson 1999, Tomkins 1999). This study suggests that much of the asymmetry of tarsi accumulates early in life (0 to 10 days after hatching) and does not decline at the end of growth. This agrees, at least in part, with patterns of asymmetry of bones in mammals, where asymmetry increases as long as the bones grow (Hallgrímsson 1999).

The causal link between increased food availability and greater symmetry remains unclear. Nestlings growing in better feeding conditions could allocate more resources to mechanisms of compensational growth that restore symmetry between the left and right tarsi. The existence of such active mechanisms of developmental control has been proposed to explain patterns of asymmetry with ontogeny (Swaddle and Witter 1997), but other processes could explain these patterns. The degree of asymmetry could not only depend on developmental errors at the microscopic level, but also on the stage of ontogeny at which the study takes place (Aparicio 1998, 2001). In the model by Aparicio (2001), traits that are more developed are expected to be more symmetric, because once the investment level reaches a certain value the high cost of growth would minimize the effect of developmental noise. However, in my study food-supplemented nestlings showed the same degree of development as control nestlings, as indicated by tarsus length. Therefore, a model that takes only the effect of ontogeny into account is less likely to explain the effect of food addition reported here, unless food addition somehow changes the shape of the relationship between investment level and trait size.

I thank the board of the National Park "De Hoge Veluwe" for permission to carry out this research. Comments by Niels Cadée, Martin Granbom and another referee improved previous versions. Arie van Noordwijk and Erik Postma gave advice about repeatability calculations. Silvia Perez provided the Spanish translation for the abstract. This study was part of a Ph.D. project partly funded by the European Commission with a Marie Curie Research Fellowship (No. ERB FMBICT 971939).

LITERATURE CITED

- APARICIO, J. M. 1998. Patterns of fluctuating asymmetry in developing primary feathers: a test of the compensational growth hypothesis. *Proceedings of the Royal Society of London Series B* 265: 2353–2357.
- APARICIO, J. M. 2001. Patterns of growth and fluctuating asymmetry: the effects of asymmetrical investment in traits with determinate growth. *Behavioral Ecology and Sociobiology* 49:273–282.
- BECKER, W. A. 1984. *A manual of quantitative genetics*. Academic Enterprises, Pullman, WA.
- BJÖRKLUND, M. 1996. The effect of male presence on nestling growth and fluctuating asymmetry in the Blue Tit. *Condor* 98:172–175.
- BJORKSTEN, T. A., K. FOWLER, AND A. POMIANKOWSKI. 2000. What does sexual trait FA tell us about stress? *Trends in Ecology & Evolution* 15:163–166.
- CHIPPINDALE, A. K., AND A. R. PALMER. 1993. Persistence of subtle departures from symmetry over multiple molts in individual brachyuran crabs: relevance to developmental stability. *Genetica* 89: 185–199.
- GIBB, J. A., AND M. M. BETTS. 1963. Food and food supply of nestling tits (*Paridae*) in Breckland pine. *Journal of Animal Ecology* 32:489–533.
- GRIECO, F. 2002. How different foraging strategies result in equal food delivery rates: an experimental study on Blue Tits. *Journal of Avian Biology* 33: 331–341.
- HALLGRÍMSSON, B. 1999. Ontogenetic patterning of skeletal fluctuating asymmetry in rhesus macaques and humans: evolutionary and developmental implications. *International Journal of Primatology* 20:121–151.
- HOFFMANN, A. A., AND P. A. PARSONS. 1991. *Evolutionary genetics and environmental stress*. Oxford University Press, Oxford, UK.
- HOVORKA, M. D., AND R. J. ROBERTSON. 2000. Food stress, nestling growth and fluctuating asymmetry. *Canadian Journal of Zoology* 78:28–35.
- KUNZ, C. 1999. Genetic variation and phenotypic plasticity in body traits of nestling Blue Tits. Ph.D. dissertation, Uppsala University, Uppsala, Sweden.
- LEARY, R. F., AND F. W. ALLENDORF. 1989. Fluctuating asymmetry as an indicator of stress: implications for conservation biology. *Trends in Ecology & Evolution* 4:214–217.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104:116–121.

- LUDWIG, W. 1932. Das Links-Rechts Problem im Tierreich und beim Menschen. Springer Verlag, Berlin.
- MØLLER, A. P., AND J. P. SWADDLE. 1997. Asymmetry, developmental stability and evolution. Oxford University Press, Oxford, UK.
- NILSSON, J.-Å. 1994. Energetic stress and the degree of fluctuating asymmetry: implications for a long-lasting, honest signal. *Evolutionary Ecology* 8: 248–255.
- NUR, N. 1984. The consequences of brood size for breeding Blue Tits II: nestling weight, offspring survival, and optimal brood size. *Journal of Animal Ecology* 53:497–517.
- O'CONNOR, R. J. 1977. Differential growth and body composition in altricial passerines. *Ibis* 119:147–166.
- PALMER, A. R., AND C. STROBECK. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Annual Review of Ecology and Systematics* 17:391–421.
- PARSONS, P. A. 1990. Fluctuating asymmetry: an epigenetic measure of stress. *Biological Review* 65: 131–145.
- PARSONS, P. A. 1992. Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity* 68:361–364.
- PERRINS, C. M. 1991. Tits and their caterpillar food supply. *Ibis* 133, Suppl. 1:49–54.
- SASVÁRI, L. 1986. Reproductive effort of widowed birds. *Journal of Animal Ecology* 55:553–564.
- STARCK, J. M., AND R. E. RICKLEFS [EDS.]. 1998. Avian growth and development. Evolution within the altricial-precocial spectrum. Oxford University Press, Oxford, UK.
- STATSOFT, INC. 1999. STATISTICA for Windows version 5.5. StatSoft Inc, Tulsa, OK.
- SWADDLE, J. P., AND M. S. WITTER. 1994. Food, feathers and fluctuating asymmetries. *Proceedings of the Royal Society of London Series B* 255:147–152.
- SWADDLE, J. P., AND M. S. WITTER. 1997. On the ontogeny of developmental stability in a stabilized trait. *Proceedings of the Royal Society of London Series B* 264:329–334.
- SWADDLE, J. P., M. S. WITTER, AND I. C. CUTHILL. 1994. The analysis of fluctuating asymmetry. *Animal Behaviour* 48:986–989.
- TEATHER, K. 1996. Patterns of growth and asymmetry in nestling Tree Swallows. *Journal of Avian Biology* 27:302–310.
- TOMKINS, J. L. 1999. The ontogeny of asymmetry in earwig forceps. *Evolution* 53:157–163.
- VAN BALEN, J. H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61:1–93.
- VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SCHARLOO. 1988. Heritability of body size in a natural population of the Great Tit (*Parus major*) and its relation to age and environmental conditions during growth. *Genetical Research Cambridge* 51:149–162.
- VAN VALEN, L. 1962. A study of fluctuating asymmetry. *Evolution* 16:125–142.
- ZAKHAROV, V. M. 1992. Population phenogenetics: analysis of developmental stability in natural populations. *Acta Zoologica Fennica* 191:7–30.

The Condor 105:603–606
© The Cooper Ornithological Society 2003

QUALITY OF FOOD SOURCE AFFECTS FEMALE VISITATION AND DISPLAY RATES OF MALE BROAD-TAILED HUMMINGBIRDS

ALAINE F. CAMFIELD¹

School of Natural Resources and Environment, University of Michigan, Dana Building, 430 E. University, Ann Arbor, MI 48109-1115

Abstract. I studied the relationships among energy availability, female visitation rates, and male display rates in Broad-tailed Hummingbirds (*Selasphorus platycercus*). Feeders contained 10%, 20%, or 30% sucrose solutions; female visitation rates and male hummingbird display rates were measured. Display rates of

male Broad-tailed Hummingbirds and visitation rates of females depended on the quality of the food source. The fact that male display rates matched female visitation rates provides further evidence that dive displays play a role in courtship. More work needs to be done to determine if the relationship between resource quality, female visitation, and male display rates shows a threshold contingent on food availability.

Manuscript received 23 May 2002; accepted 12 February 2003.

¹ E-mail: camfield@umich.edu

Key words: *Broad-tailed Hummingbird, display rates, female visitation, food quality, Selasphorus platycercus.*

La Calidad de los Recursos Alimenticios Afecta las Tasas de Visita de las Hembras y de Despliegues de Cortejo de los Machos en *Selasphorus platycercus*

Resumen. Evalué las relaciones entre la cantidad de energía disponible, la tasa de despliegues de cortejo por parte de los machos y la tasa de visita por parte de las hembras en *Selasphorus platycercus*. Para los comederos utilicé soluciones de agua azucarada en concentraciones de 10%, 20% ó 30%, y medí las tasas de visita de las hembras y de despliegues de cortejo de los machos en cada período de observación (1 hora por período). Las tasas de cortejo de los machos y de visita de las hembras dependieron de la calidad de los recursos alimenticios. El hecho de que las tasas de despliegue de los machos se relacionaran directamente con las tasas de visita de las hembras indica la importancia de los despliegues de caída libre durante el cortejo en esta especie. Se necesitan más investigaciones para determinar si la relación entre la calidad de recursos alimenticios, las visitas de las hembras y las tasas de despliegue presenta un límite relacionado con la disponibilidad de alimento por encima del cual la forma de esta relación se modifica.

Many hummingbird species perform spectacular, energetically expensive displays, generally recognized as playing a role in courtship and agonistic interactions (Tamm et al. 1989). The displays of the Broad-tailed Hummingbird (*Selasphorus platycercus*) are characterized by a series of climbs and dives. These hummingbirds may climb up to 30 m in height before diving, and as they descend their characteristic wing-trill can be heard, along with a vocalization at the bottom of the dive (Calder and Calder 1992).

Because male hummingbird displays are energetically expensive, they should depend to some degree on the energy available to the individual (Tamm 1985). In addition, since male hummingbird displays are usually prompted by the presence of a female (Tamm et al. 1989, Hurly et al. 2001), display rates should also depend on the number of females present.

To investigate this possibility, I manipulated the quality of Broad-tailed Hummingbird food sources and examined relationships among food richness, female visitation rates, and display rates of males. I expected to see higher female visitation rates at higher quality sites; and as a result of increased female presence, I expected to see more male displays at high quality sites than low quality sites.

METHODS

STUDY AREA

I studied Broad-tailed Hummingbirds in the Gunnison National Forest in Gunnison County, Colorado, approximately 4 km upstream from the Rocky Mountain Biological Laboratory in Gothic, Colorado (2900 m elevation, 38°58'N, 106°59'W). The surrounding area is a mix of subalpine meadows, aspen (*Populus tremuloides*) stands, and riparian corridors of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*; Calder et al. 1983). I placed nine feeders

(Perky-Pet Products Co., No. 215 Hummingbird Feeder, Denver, Colorado) at least 50 m apart, along a 1-km stretch on the eastern side of the valley. Each feeder was placed near running water, either on the edge or in the middle of an open meadow next to willows (*Salix* spp.) or conifers.

The study took place between 28 May and 6 August 2001. Feeders were set up on 28 May and the first data were recorded 30 May. On 6 June feeders 1, 2, 8, and 9 were moved to nearby locations to avoid disturbing other researchers. No effect on hummingbird behavior was noted.

The feeders held 100 mL of solution, had only one feeding opening, and no perch, so the birds had to hover while feeding. Feeders were hung on metal poles 1.5 m above the ground. Sucrose concentrations (10%, 20%, and 30% weight per volume) were assigned to sites using a random number table: feeders 1, 4, and 6 were assigned 10% sucrose solutions, feeders 3, 8, and 9 were assigned 20% sucrose solutions, and feeders 2, 5, and 7 were assigned 30% sucrose solutions. Feeders were filled daily, and did not receive direct sunlight until about 08:30–09:00.

DATA COLLECTION

My field assistant and I observed each feeder daily for 1 hr between 06:30 and 14:00. Observations were made 6–7 m from the feeders. Feeders 1–5 were observed on one day, feeders 6–9 the next. During the season we made a total of 17 visits to each feeder, and we rotated the time of observation at each feeder to avoid temporal associations of activity levels.

We recorded the number of female Broad-tailed Hummingbird visits to each feeder, and counted the number of mating displays performed by males during each observation period at each site. The birds were not individually marked.

STATISTICAL ANALYSIS

The dependent variables used in the analysis were not normally distributed. The counts of female visits and male displays were modeled using a negative binomial distribution, which is appropriate for non-normal count data (Gardner et al. 1995). The analysis took into account the lack of independence of repeated observations from the same site using generalized estimating equations (GEE; Diggle et al. 1994).

Results of GEE analysis are reported as χ^2 values. This analysis allowed for *post-hoc* comparisons of the three treatments, and using the Bonferroni correction for multiple comparisons, alpha was set at 0.02. Means are reported \pm SE. All analyses used Proc Genmod in SAS release 8.2 for Windows (SAS Institute Inc. 2001).

RESULTS

Female Broad-tailed Hummingbirds visited high quality feeders more often than low quality feeders. Females made 0.3 ± 0.1 visits hr^{-1} at 10% feeders ($n = 48$; range 0–5), 4.2 ± 0.8 visits hr^{-1} at 20% feeders ($n = 49$; range 0–35), and 5.8 ± 1.0 visits hr^{-1} at 30% feeders ($n = 48$; range 0–37; Fig. 1a). There were significantly more female visits to sites with 20% feeders than sites with 10% feeders ($n = 97$, $\chi^2_1 = 28.1$, $P < 0.001$). There were also significantly more female

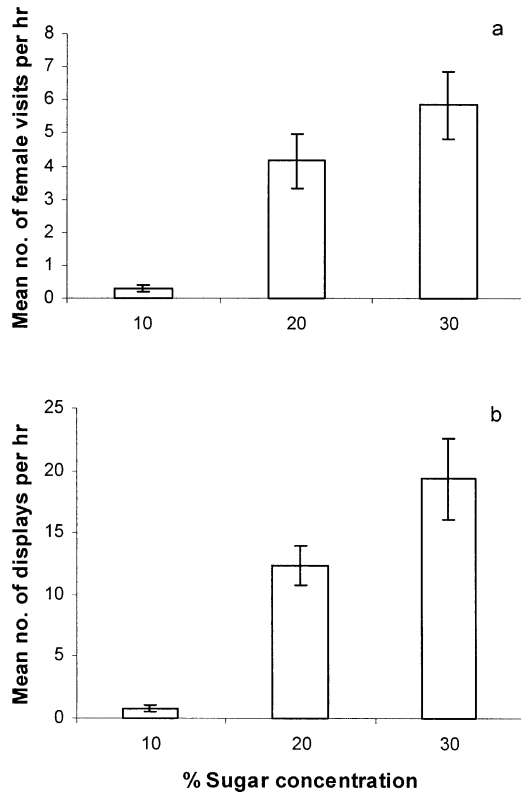


FIGURE 1. (a) Mean (\pm SE) number of visits per hour by female Broad-tailed Hummingbirds to feeders of three concentration levels (10%, 20%, and 30% sucrose solutions). Females visited high quality feeders more often than low quality feeders. (b) Mean (\pm SE) display rate of male Broad-tailed Hummingbirds at the same feeders. Males defending high quality feeders displayed more often than males defending low quality feeders.

visits to sites with 30% feeders than sites with 10% feeders ($n = 96$, $\chi^2_1 = 41.3$, $P < 0.001$). However, there was no significant difference between the number of female visits per hour at the 20% and 30% feeders ($n = 97$, $\chi^2_1 = 3.0$, $P = 0.08$).

Male display rates showed a pattern similar to that of female visitation rates. Male Broad-tailed Hummingbirds performed more displays at high quality feeders than low quality feeders: 0.8 ± 0.3 displays hr^{-1} at 10% feeders ($n = 42$; range 0–11), 12.3 ± 1.6 displays hr^{-1} at 20% feeders ($n = 41$; range 0–44) and 19.4 ± 3.2 displays hr^{-1} at 30% feeders ($n = 46$; range 0–92; Fig. 1b). Male Broad-tailed Hummingbirds displayed significantly more often at sites with 20% feeders than sites with 10% feeders ($n = 83$, $\chi^2_1 = 19.3$, $P < 0.001$) and they displayed significantly more often at sites with 30% feeders than sites with 10% feeders ($n = 88$, $\chi^2_1 = 19.4$, $P < 0.001$). However, there was no significant difference in display rates at sites with 20% and 30% feeders ($n = 87$, $\chi^2 = 0.7$, $P = 0.4$).

These results suggest that there may be a threshold level beyond which an increase in energy availability does not affect female visitation or male display rates.

The number of observation periods with no displays varied across feeder concentrations, with 35, 8, and 7 zero values at 10%, 20%, and 30% feeders respectively. The large number of zero values at the 10% feeders may reflect the fact that low concentrations of sugar solutions do not attract as many females as high concentrations; or they may not provide sufficient energy for males to sustain a high display rate.

DISCUSSION

Display rates of male Broad-tailed Hummingbirds reflected the number of females they encountered. Female visitation rates, in turn, depended on the quality of the food source. These findings support the hypothesis that males on high quality sites encounter more females than males on low quality sites, and therefore display more frequently. The fact that male display rates reflect female visitation rates provides further evidence that dive displays function in courtship (Hurly et al. 2001), rather than primarily in territory defense as suggested by Stiles (1982). An alternate explanation of the results is that male Broad-tailed Hummingbirds displayed more directly as a result of increased energy availability, rather than indirectly as a function of female presence.

My study suggests that the relationship between energy availability, female visitation rates, and display rates may not be linear, but rather may show a threshold pattern. Beyond an upper threshold, increases in energy availability may have no effect on the number of female visits or male display rates. It seems logical that thresholds in male display rates will be reached since at some point the birds must devote their attention to activities other than courtship; regardless of energy availability, hummingbirds cannot perform an endless loop of dive displays.

Among other aspects of hummingbird behavior, territoriality has been shown to depend on threshold levels of energy availability (Ewald and Carpenter 1978, Kodric-Brown and Brown 1978). Tamm (1985) found that display rates of male Calliope Hummingbirds (*Stellula calliope*) increased with the amount of food supplied. However, Tamm did not provide food sources of varying quality; he added feeders with a 20% sucrose solution to existing territories. It is possible that a threshold exists between the normal range of energy available at natural sites and Tamm's augmented sites, but Tamm's two-level study design would not have detected this.

More work needs to be done in this area. The data presented here suggest that a threshold may exist, but more than three categories are required to provide conclusive evidence and to investigate the statistical vs. biological significance of such a threshold.

Powers (1987) manipulated food supply on territories of male Anna's Hummingbirds (*Calypte anna*) and failed to find a relationship between sucrose concentration and display frequency. However, Powers conducted energy manipulation experiments inside previously mapped territories. It is possible that the energy available on the sites was at a relatively high level

before any manipulations were done. Hence, the addition of feeders would not affect display rates. Conversely, Powers' choice of concentrations (0%, 4%, 8%, 12%, 16%, and 20% sucrose solutions) leaves open the possibility that male Anna's Hummingbirds require a higher concentration than 20% to raise display rates. Further, Powers did not test for a threshold between display frequency and sucrose concentration, a pattern suggested by his figures.

A potentially confounding variable in my study is that natural variation in food abundance around the territories was not quantified. Although I attempted to establish sites in areas with equivalent levels of natural food sources, it is possible that the birds responded to natural variation that was not measured.

I found clear relationships among female Broad-tailed Hummingbird visitation rates, male display rates, and the quality of their supplemental food source. Increases in sucrose concentration led to an increase in female presence and increased male display rates. More work needs to be done to determine if a threshold relationship indeed exists between territory quality, female visitation rates, and male display rates in Broad-tailed Hummingbirds.

I would like to thank Jennie Edgar for her invaluable assistance in the field and the Rocky Mountain Biological Laboratory for permitting me to use their facilities. Also, thanks to Bobbi Low, Johannes Foufopoulos, and several anonymous reviewers for their help revising this document; and Kathy Welch for her help with statistical analyses. Support for this study was provided in part by the Lee R. G. Snyder Memorial Fund.

LITERATURE CITED

- CALDER, W. A., AND L. L. CALDER. 1992. Broad-tailed Hummingbird (*Selasphorus platycercus*). In A. Poole, F. Gill, and P. Stettenheim [EDS.], *The birds of North America*, No. 16. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- CALDER, W. A., N. M. WASER, S. M. HIEBERT, D. W. INOUE, AND S. MILLER. 1983. Site-fidelity, longevity, and population dynamics of Broad-tailed Hummingbirds: a ten-year study. *Oecologia* 56: 359–364.
- DIGGLE, P. J., K. Y. LIANG, AND S. L. ZEGER. 1994. *Analysis of longitudinal data*. Clarendon Press, Oxford Science Publications, Oxford, UK.
- EWALD, P. W., AND F. L. CARPENTER. 1978. Territorial responses to energy manipulations in the Anna Hummingbird. *Oecologia* 31:277–292.
- GARDNER, W., E. P. MULVEY, AND E. C. SHAW. 1995. Regression analysis of counts and rates: Poisson, overdispersed Poisson, and negative binomial models. *Psychological Bulletin* 118:392–404.
- HURLY, T. A., R. D. SCOTT, AND S. D. HEALY. 2001. The function of displays of male Rufous Hummingbirds. *Condor* 103:647–651.
- 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.
- POWERS, D. R. 1987. Effects of variation in food quality on the breeding territoriality of the male Anna's Hummingbird. *Condor* 89:103–111.
- SAS INSTITUTE INC. 2001. *SAS/STAT user's guide*. Release 8.2. SAS Institute Inc., Cary, NC.
- STILES, G. F. 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. *Behavioral Ecology and Sociobiology* 16:203–207.
- TAMM, S., D. P. ARMSTRONG, AND Z. J. TOOZE. 1989. Display behavior of male Calliope Hummingbirds during the breeding season. *Condor* 44:272–279.