lieves this record likely refers to the Whimbrel (*N. phaeopus*).

As far as we know, the present photographic evidence represents the first confirmed record of the Long-billed Curlew for continental South America. One copy of the color photograph has been deposited in the Colección Ornitologica Phelps in Caracas, and one is in the Ornithological Collection, Department of Biological Sciences, University of Montreal.

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Survivorship in Hummingbirds: Is Predation Important?

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The traditional optimal foraging models reviewed by Pyke et al. (1977) and Krebs (1978) focused on proximal factors that influence energetic costs and benefits in terms of their contributions to net rate of energy gain. In general, these models have assumed that the fitness value of foraging tactics is determined primarily by proximal factors such as quality and distribution of food patches, although a variety of other factors such as cryptic prey, territory defense, or predation risk also may significantly affect feeding rates (Caraco 1980). For example, sticklebacks (*Gasterosteus aculeatus*) alter their foraging tactics and feeding rates when predators are present (Milinski and Heller 1978), and feeding Blue Tits (*Parus caeruleus*) increase their scanning rates as predation risk increases (Leuchem 1983).

In a more general context, McCleery (1978) reviewed attempts to study how time budgets and behavior sequences are influenced by costs and benefits under conditions of conflicting demands. He concluded that to be accurate and predictive, optimization models and their associated decision rules must account for elements in the environment that constrain performance and significantly affect the expression of particular choices.

An advantage in the study of the behavioral ecology of nectar-feeding birds, and hummingbirds in particular, is the relative simplicity of the foraging system and the extent to which it lends itself to reasonably direct and uncomplicated field and laboratory measurements and experiments (Hainsworth 1981). It is an energy-limited system (Carpenter 1978, Gass and Montgomerie 1981) in which the amount and energy content of the food is easily measured in the field, the food sources are stationary and conspicuous, and the foraging behavior of these diurnal birds is easily observed (Gass and Montgomerie 1981). In this paper we review the literature of predation on hummingbirds for evidence of consistent amounts or patterns that would indicate that predation is a significant mortality factor.

Observed predation.—Table 1 shows the North American records of predation on "adult" hummingbirds (of unknown age from fledging) that are available from the literature. This does not include 4 records of hummingbirds caught in spider webs (Danforth 1921, Woods 1934, Stott 1951, Hoyt 1960) and one attacked by wasps (Grant 1959). The 13 recorded instances of predation involve 4 identified species of hummingbirds and a variety of predators (9), including insects, amphibia, and birds. Most of the instances listed in Table 1 occurred in flower gardens (7) or at hummingbird feeders (2). In the cases of predation by frogs and birds, the hummingbirds were eaten, but not by the mantids.

It is especially noteworthy that there are only 3 recorded instances of predation by raptors, and these cases were distributed among 3 raptor species. When Lowery (1938) found the remains of a Ruby-throated Hummingbird (*Archilochus colubris*) in the stomach of

TABLE 1. North American records of predation on hummingbirds.

Predator	Hummingbird	Instances	Source
Insecta			
Mantidae			
Tenodera ardifolia	*Archilochus colubris*	2	Butler 1949, Hildebrand 1949
Amphibia			
Ranidae			
Rana pipiens	*A. colubris*	3	Norris-Elye 1944
Rana sp.	*Selasphorus rufus*	1	Morgan 1947
Aves			
Accipitridae			
Accipiter striatus	*Calypte anna*	1	Peters 1963
Falconidae			
Falco columbarius	*A. colubris*	1	Lowery 1938
Falco sparverius	*A. colubris*	1	Mayr 1966
Cuculidae			
Geococcyx californianus	*A. alexandri*	1	Spofford 1976
Tyranninae			
Myiarchus tyrannulus	*S. rufus*	1	Gamboa 1977
Icterinae			
Icterus galbula	*Selasphorus* sp.	1	Ashman 1977
	A. colubris	1	Wright 1962

a Pigeon Hawk (*Falco columbarius*), he conducted an extensive search of the files of the Bureau of Biological Survey and found that this was the first record of a hummingbird in the stomach of any bird, all raptors included. It could, of course, be argued that most recorded instances of predation on hummingbirds are from gardens or at hummingbird feeders because of the higher probability of predation being observed in such situations, and that natural predation is important but seldom seen. This argument is not particularly convincing in view of the exponential increase in field research on hummingbirds in the last decade (Montgomerie and Gass 1980) and the lack of a corresponding increase in reports of predation.

The fact that there have only been 13 reports of predation on hummingbirds since the first by Lowery in 1938, that many of these instances can be classified as unusual or even bizarre, and that there is no consistent pattern in predator-prey relationships or amounts of predation suggests that these are isolated incidents, and that hummingbirds in North America do not have "natural predators" in the usual sense.

The only systematic predation on hummingbirds that has been reported in the literature is from the tropics, by Bat Falcons (*Falco albigularis*). Beebe (1950) monitored the activities of a pair of Bat Falcons at the Rancho Grande in the National Park at Aragua, Venezuela, for 5½ months, during which time they were seen to kill and/or bring to the nest 34 individuals of 10 species of hummingbirds ranging from the small *Chaetocerus jourdanii* (69 mm total length) to larger, relatively slow-flying Booted Racquet-tails (*Ocreatus underwoodii*). Although this pair of falcons killed a wide variety of mammals, birds, reptiles, amphibia, and insects (78 species), birds constituted 71.8% of the species (56) and 74.8% of the individuals (163) in the total recorded diet. Of the total birds, 17.8% of the species and 20.8% of the individuals were hummingbirds. Stiles (1978) commented that Bat Falcons apparently are generalists, with no behavioral or other specializations for preying on hummingbirds. However, considering the fact that the single pair observed by Beebe (1950) captured 4 species of bats, 8 species of swifts, 2 species of swallows, and 10 species of hummingbirds in flight indicates that they are effective predators on fast-flying, small prey.

Beebe (1950) estimated that this pair of Bat Falcons killed at least 600 birds and bats during his 164 days of observation. On the basis of their proportion in the recorded sample, this would include over 100 hummingbirds. It would seem, therefore, that Bat Falcons could be significant hummingbird predators in the tropics, even though they are not necessarily hummingbird specialists. Bat Falcons are quite common over most of their latitudinal range of 48°, from central Mexico to southern Brazil and northern Venezuela (Beebe 1950), which includes the geographical distributions of many species of hummingbirds (Greenewalt 1960).

Stiles (1978) has postulated, on the other hand, that the Tiny Hawk (*Accipiter superciliosus*) may be a hummingbird specialist. This small, fast-flying accipiter apparently locates perches that are frequently used by territorial hummingbirds and waits in conceal-

ment to capture them when they return to perch. While this hypothesis is plausible, it is based on only one observation of a successful attack on *Amazilia tzacatl* and a few unsuccessful attacks on *Chalybura urochrysia*; more data will be required to establish its validity. There is no evidence that predation by Bat Falcons, Tiny Hawks, or other predators in the wintering areas of North American immigrants affects their mortality rates or behaviors, but this is a possible factor that should be considered.

Natural longevity.—If predation plays a minor role in the mortality rates of adult hummingbirds, one might expect that this would be reflected in their natural longevities. From available equations for variables using hypothetical body masses and scaling components, Brown et al. (1978) calculated that a hypothetical hummingbird weighing 3 g should have a life span of 5.5–5.8 yr and a 4-g bird should have a life span of 5.8–6.1 yr (see also Lindstedt and Calder 1976, 1981). These predictions assume a balanced energy budget and do not include the possible negative effects of extrinsic factors such as disease, nutrition, weather, or predation on life expectancy. In other words, this is essentially an estimate of physiological longevity based on energy requirements and expenditures, without regard to other mortality factors that might affect life expectancy.

Hummingbirds have not been banded as systematically as most other birds, and in any case it is highly unlikely that band recoveries would occur except through recapture. Consequently, return rates are usually low, and relatively little is known about the natural longevities of hummingbirds. Clapp et al. (1983) listed longevity records for only 4 species: *Archilochus colubris* (6 yr, 3 months), *Calypte anna* (6 yr), *Selasphorus platycercus* (7 yr, 1 month), and *S. sasin* (3 yr, 11 months) based on recaptures of birds of unknown age at the time of banding.

The most important and only systematic analysis of the natural longevity and population dynamics of hummingbirds is a study of Broad-tailed Hummingbirds (*S. platycercus*) banded between 1972 and 1980 at the Rocky Mountain Biological Laboratory (RMBL) at Gothic, Colorado (Calder et al. 1983). These birds showed strong site-fidelity, with recapture rates between breeding seasons as high as 70% for females and 27% for males. During this study, 2 females were recaptured that were at least 8 yr old and 1 male that was at least 5 yr old (age unknown when banded). During the 1983 field season, 2 more females of the same age were recaptured, bringing the total number of 8-yr-old birds to 4 (D. Inouye pers. comm.). Calder et al. (1983) calculated that the mean age of females recaptured in 1979 and 1980 was 3.1 yr ($n = 58$) and for males 2.6 yr ($n = 23$). In a preliminary report on the RMBL hummingbird population, Waser and Inouye (1977) estimated a mean life span of at least 2.5 yr for both sexes combined.

Elder and Zimmerman (1983) compared estimates of the mean life spans of Black-capped Chickadees (*Parus atricapillus*) based on recaptures or resightings and found a considerable discrepancy between the two sources of data; the same method of estimation gave a mean life span of 2.6 yr from resightings and 1.7 yr from recaptures. They also found that older birds tended to avoid recapture more than young birds, which could be a particularly serious factor with hummingbirds because they quickly learn to avoid mist nets (pers. obs.). This suggests that the life spans calculated by Calder et al. (1983) from recaptures might be an underestimate.

More importantly, the oldest broad-tails recorded so far seem remarkably long-lived, compared with predictions based on body mass, and as it was only during 1979 and 1980 that most of the local population was banded (Calder et al. 1983), it is likely that recorded natural longevity will be extended further in the near future. If predation on adult hummingbirds were important, we would not expect maximum life spans that are so much greater than physiological expectations.

Other sources of mortality.—W. A. Calder (pers. comm.) used the data in Calder et al. (1983) to calculate a difference of 6.1 yr between physiological life span and the realized longevity of the Broad-tailed Hummingbirds at RMBL. While there is limited evidence of adult hummingbird mortality due to migration fatalities, disease, and accidents (W. A. Calder pers. comm.), nesting failure may be a very important source of mortality in hummingbird populations. Baltosser (1983) monitored 148 nests of Black-chinned (*Archilochus alexandri*), Broad-billed (*Cyanthus latirostris*), Violet-crowned (*Amazilia violiceps*), and Costa's (*Calypte costae*) hummingbirds and found a 59% failure due to nest abandonment, egg mortality, and nestling mortality. The most serious factors were egg and nestling predation, which accounted for 58.6 and 25.3% of the observed losses.

Calder et al. (1983) defined "nesting success" as fledging of at least 1 young from a nest in which eggs were laid (mean clutch size = 2). During their study nesting success varied from 18 to 67% (mean = 46% of all nests).

There are no data available on the period between fledging and self-sufficiency, but this could be an extremely critical period in the early life of a bird with such high energy requirements.

Conclusion.—On the basis of the available data, we conclude that the observed predation on adult hummingbirds in temperate habitats shows no consistent amount or pattern that would indicate that predation is a significant risk factor, and biologists have been justified in ignoring predation in the decision rules specified for these species. This conclusion ignores the importance of nestling mortality (Calder 1973, Calder et al. 1983) and is based solely upon observed rates of predation on foraging adults. It is, however, quite possible that this assumption would be unjustified for hummingbirds in the Neotropics, where Bat Falcons, Tiny Hawks, and other predators might

impose significant mortalities that could be reflected in foraging strategies.

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