

## AN EXTRA-LIMITAL BROAD-TAILED HUMMINGBIRD IN WINTER: DISORIENTED OR HARBINGER OF CHANGE?

WILLIAM A. CALDER

*Department of Ecology and Evolutionary Biology  
University of Arizona  
Tucson, Arizona 85721 USA*

**Abstract.**—Factors that might limit distribution and ability to thermoregulate were examined in a male Broad-tailed Hummingbird (*Selasphorus platycercus*) wintering in Arizona, unusual for this species. As in the breeding season, territorial activity and feeding did not begin until incident daylight intensity exceeded 11 lux. The daylength available for attaining positive energy balance was one-third shorter than in the summer. Meal size increased through the day. By evening, cumulative intake of sucrose was sufficient to fuel maintenance of a high, non-torpid, temperature for 14 h of nocturnal fast, even without the small flying insects and nectar from introduced *Salvia*, taken to supplement the feeder solution. In contrast to the subordinate status of broad-tails wintering in Mexico, this bird excluded larger Anna's and smaller Costa's Hummingbirds from his territory. His January–February molt timing was similar to that of a population wintering in Jalisco, fitting the annual cycle of northern breeders. The Tucson male returned the following autumn, proving his ability for extralimital survival and orientation.

### UN SELASPHORUS PLATYCERCUS INVERNANDO FUERA DE LIMITES: ¿DESORIENTADO O ANUNCIADOR DE CAMBIO?

**Sinopsis.**—Se examinaron factores que puedan limitar la distribución y la habilidad para termorregularse en un *Selasphorus platycercus* macho invernando en Arizona, poco usual en esta especie. Como en la época de apareamiento, la actividad territorialista y la alimentación no empezó sino hasta que la intensidad de luz diurna incidental sobrepasaba las 11 unidades lux. El largo de día accesible para obtener un balance de energía positivo era un tercio más corto que en el verano. El tamaño de la comida aumentó a través del día. Por la tarde el ingreso acumulado de sucrosa era suficiente para mantener una temperatura alta, no en torpor, por 14 horas de ayuno nocturno, inclusive sin los pequeños insectos voladores y el nectar de la *Salvia* introducida suplementando la solución de comederos. En contraste a la condición subordinada de los *Selasphorus platycercus* invernando en México, este ave excluyó colibríes como *Calypte anna* (mayor) y *C. costae* (menor) de su territorio. Su tiempo de muda entre enero y febrero fue similar al de una población invernando en Jalisco, ajustándose al ciclo anual de los anidantes del norte. El macho de Tucson retornó el otoño posterior, demostrando su extralimitadas capacidades de supervivencia y orientación.

Individual birds, encountered beyond seasonal or geographical limits of species' distribution ("extra-limits"), excite field ornithologists. Generally missing from the excitement, however, has been discussion of the relationship of possibly risky extralimital occurrence to the evolution of distribution range. Why are they here? (How) do they survive? A bird might be "extralimital" or "accidental" because it was (1) disoriented, (2) unable to store enough fat for normal completion of migration, (3) displaced from migration route by weather, (4) flight-impaired or (5) an escaped captive. Alternatively, the bird could have been (6) a potential pioneer, however unwittingly.

Small size and associated energetic constraints make hummingbirds seem unlikely prospects for survival beyond their normal environments. Nevertheless, extralimital observations of hummingbirds are now fre-

quent, perhaps related to availability of artificial feeders and cultivated flowers. Anna's Hummingbird (*Calypte anna*) was once essentially limited to California (Bent 1940), but appeared in Seattle, Washington in 1964. Three were reported in winter 1970–1971, and 15 on the 2 Jan. 1993 Christmas Census (Mattocks 1993, Zimmerman 1973). If previously constrained by energy balance problems, distributions may change with anthropogenic climate change. Hence some extralimitals could function as indicators of climate change. Womack (1993) compiled a preliminary list of "extralimital hummingbirds" reported between 1988 and 1993. As she indicated, some reports may be erroneous or duplicates. Others may have been merely tardy transients that did not stay all winter. Extra-limitalism is common, even with deletion of some of the >900 records.

Valuable insight may await us in the study of extra-limitals. Standard references describe winter ranges but provide little information on how birds function for three quarters of the year. The Broad-tailed Hummingbird (*Selasphorus platycercus*) normally winters from northern Mexico highlands, southward into the mountains of central and southern Mexico. It is only rarely seen as far north as Big Bend National Park, Texas (American Ornithologists' Union 1983, Johnsgard 1983). Davis and Russell (1990) cited three broad-tail records from southern Arizona in December, but no January records to indicate that these birds survived the winter.

By wintering 20° south of typical Colorado breeding sites, the broad-tail can not only find flowers in mid-winter, but gain 1.4 h of additional daylight for feeding (Calder and Calder 1992). Survival of such a very small bird north of its normal winter range provided a unique opportunity to evaluate distributional constraints imposed by temperature, energy supply, daylength and interspecific biology.

I located the winter territory of an adult male Broad-tailed Hummingbird on 24 Nov. 1990, in a small fragment of native desert-scrub vegetation in a suburb on Tucson's north side. Normally, broad-tails are seen in this habitat only during spring migration; in the Santa Catalina Mountains north of Tucson, broad-tails are not observed until late February at the earliest (Calder 1974). I monitored his body mass, behavior and relevant physical variables to analyze his winter situation.

#### METHODS

*Site.*—This male (band T22474, 2 December) had claimed a territory in a residential front yard, at 780 m elevation on the southern bajada of alluvium from the Santa Catalina Mountains. The native Sonoran desert-scrub vegetation (Lower Sonoran [Lowe 1967]), now restricted to about one-fifth of its original area by houses, driveways and landscaping, included foothill paloverde (*Cercidium microphyllum*), mesquite (*Prosopis juliflora*), white-thorn (*Acacia constricta*), graythorn (*Ziziphus obtusifolia*), staghorn cholla (*Opuntia versicolor*), prickly pear (*Opuntia phaeacantha*), saguaro (*Carnegia giganteus*) and bur-sage (*Franseria deltoidea*).

Introduced as a landscaping plant, *Salvia greggii* bloomed profusely and attracted the broad-tail, Anna's (resident; breeding in January–February)

and Costa's (*Calypte costae*) Hummingbirds until the flowers were nipped by record cold weather ( $-4$  C) on 23 December. On 1 December, nectar samples from the *Salvia* had an average optical density equivalent to a 38 per cent (by weight, = 1.3 mol/l) sucrose solution. The broad-tail obtained an unmeasured portion of his diet from small flying insects, but his energy balance was heavily subsidized by a feeder (Perky-Pet "Little Beginner" #214) containing solutions varying from 28 to 36% sucrose (0.97 to 1.25 mol/l). This was, without doubt, crucial to his energy balance after the demise of the *Salvia*. Nectar and feeder solution concentrations were measured with a pocket refractometer (Atago N2, range 28–62%, calibrated to a reference saline solution).

*Observations.*—I recorded arrivals ( $n = 41$  d), daytime activity and feeding ( $n = 8$  d, 1 d continuous dawn-dusk), and last activity ( $n = 25$  d) at intervals of 2 to 6 d, 1–20 Dec. 1990 and 11 Jan.–24 Feb. 1991 (3 wk absence to study broad-tails wintering in Jalisco). I timed events with a chronometer-stopwatch set to National Bureau of Standards Radio WWV. The broad-tail's arrival at dawn from the northeast (roost site unknown) was signalled by his inbound wing trill (until molting) and by rapid vocal chipping as he approached and perched in a paloverde or acacia. I measured light intensity with a Gossen "Luna-Pro" light meter with diffusing hemisphere, the logarithmic scale of which was readable to the nearest 0.9 lux in the 11–22 lux ambient range of first activity.

I monitored air temperatures to  $\pm 0.5$  C with a mercury max-min thermometer suspended 1.5 m above ground, approximating his dawn perching height. These local minima correlated well ( $r = 0.89$ ;  $P < 0.001$ ;  $n = 38$ ), averaging 0.1 C warmer (range  $\pm 4$  C), than the National Weather Service low recorded 30 km south and 50 m lower in the Tucson thermal inversion. During my 3-wk absence in Mexico for field work, the minimum at the site was  $-4$  C; the official low on 23 December was  $-6$  C (Fig. 1).

*Weighing.*—I determined body mass via a perch affixed to the pan of an electronic balance (Carpenter et al. 1983). The Mettler PE-300-SE remote-reading balance was readable to 0.01 g, tared often to correct for zero drift, and within  $\pm 0.01$  g (checked against reference masses at day-break, mid-day, and when temperature or other changes warranted reassurance). A 5-s averaging function on the balance dampened fluctuations during windy periods. Once the bird was accustomed to my presence near the feeder, I substituted a more convenient battery-powered balance (Ohaus CT200, reliable to 0.01 g and checked as above) for dawn and final weighings.

#### RESULTS AND DISCUSSION

*Daylength utilization and territorial behavior.*—Feeding onset at dawn appeared to be a function of incident light, rather than ambient temperature (note greater variability in low temperatures [Fig. 1] than for light intensities and arrival times on territory for the first, modest meal [Fig. 2a]). This was similar in pattern to breeding males' first activity during

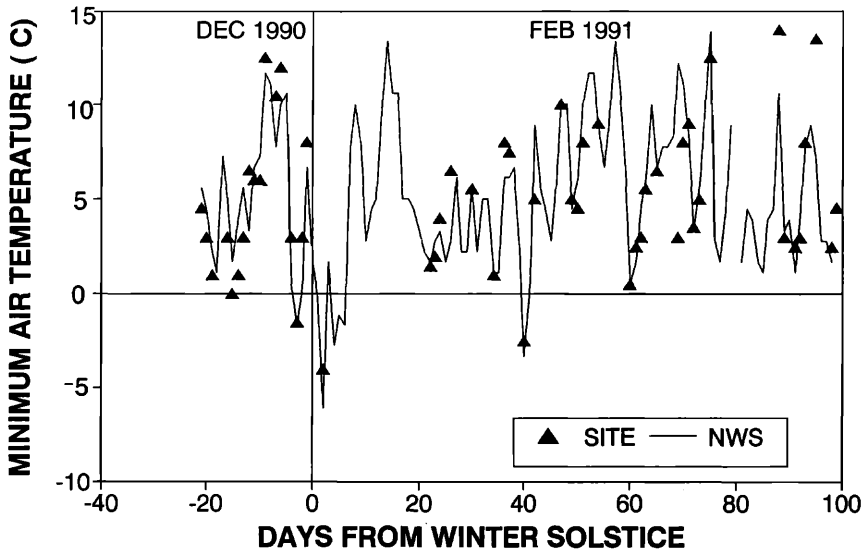


FIGURE 1. Dawn air temperatures on the winter territory of a male Broad-tailed Hummingbird (triangles) may be compared to the National Weather Service official low temperatures for Tucson during the winter of 1990–1991. The low on 23 December (2 d after winter solstice) was a new record for that date.

the summer in Colorado, where males returned from nocturnal roosts about 18 min before sunrise, at 11 lux average incident light intensity. After the summer solstice, first activity coincided roughly with 11 lux intensity as days shortened (Calder 1975). In winter, the Tucson bird returned to his territory at a mean light intensity of 18 lux ( $\pm 7.2$  SD), averaging only 1.8 min after 11 lux was recorded (Fig. 2A). Thus his winter activity could have been predicted from ambient light intensity.

I expected him to need to exploit the entire winter daylength in Tucson, since it was  $\approx 4$  h shorter than the summer activity-daylength at 39°N, but he abandoned his territory 1 h or more before sunset on several occasions (Fig. 2B). Perhaps he was feeding elsewhere, but the lower activity level when not breeding and access to unlimited feeding had already allowed adequate refuelling in 10 h to support an 14 h nocturnal fast, permitting early diurnal abandonment of territory (calculations below).

Migrant hummingbirds, including the broad-tail, subordinate to resident species (many of which are larger) while wintering in the Volcan de Colima region of south-western Mexico (DesGranges 1979, DesGranges and Grant 1980). The Tucson broad-tail, however, did not defer to Anna's Hummingbirds, whose average body mass was 24% larger (4.44 g). Anna's or Costa's were promptly chased away by the broad-tail if they approached the *Salvia* or feeder. They were able to feed there only before the broad-tail arrived at first light, during his infrequent mid-day absences, and after he departed for the night.

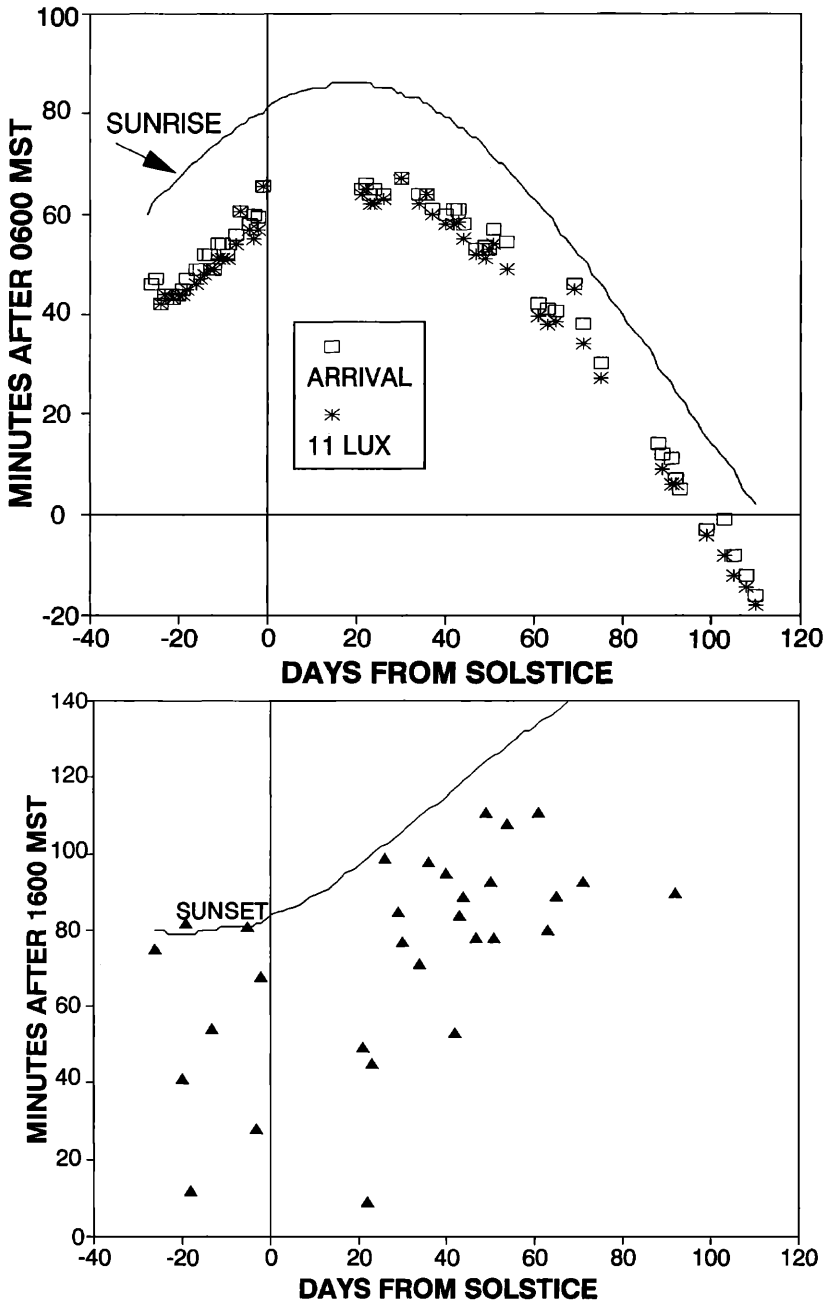


FIGURE 2A. The time of arrival by a male Broad-tailed Hummingbird on his winter territory is indicated by squares. Each \* signifies the time at which light intensity reached 11 lux.

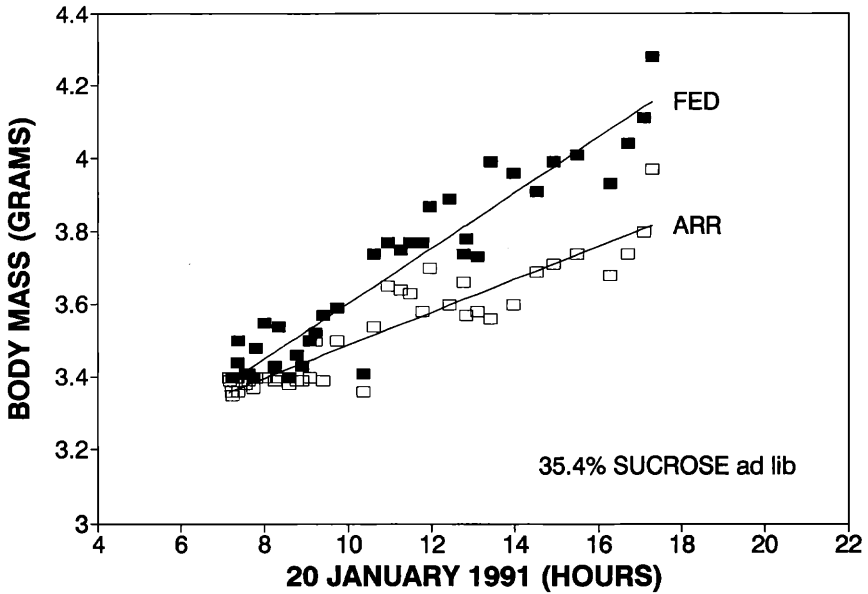


FIGURE 3. The body mass of the wintering male was recorded upon arrival (empty squares, ARR) and at conclusion of each meal (filled squares, FED). The slope of the regression for ARR is assumed to represent gradual fat accumulation from previous meals. By 1700 hours, this is calculated to be sufficient to meet the energy cost of nocturnal homeothermy. Thus hypothermic torpor does not appear to be necessary (see text). Slope differences between regression lines suggest a tendency for meal sizes to increase progressively through the day.

*Food intake and body mass patterns.*—Mass gains were evaluated in the context of (a) published data for the same species breeding in Colorado and wintering in Mexico, and (b) total energy intake compared with doubly-labelled water determinations for the Anna's Hummingbird. I assume that gains represented lipid storage, for reasons given in Calder (1994).

During the breeding season, territorial male broad-tails gain only 2–3 mg/h, adding less than 2% to body mass all day. This weight-control facilitates rapid acceleration and territorial performances. Not until dusk do they indulge in a burst of intense feeding (Calder et al. 1990). Nesting females gained steadily through the day at a rate of  $15 \pm 2.3$  mg/h (Calder 1994, Calder and Calder 1992). In a wintering population on Volcan

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The upper line shows time of local sunrise. This relationship between light intensity and onset of territorial activity is indistinguishable from summer behavior, except that the daytime activity period is considerably shorter. 2B. The male Broad-tailed Hummingbird usually abandoned his winter territory and departed (triangles) well in advance of local sunset (upper curve).

Nevado de Colima, Jalisco, Mexico, capture body masses of both sexes tended to increase progressively on an hourly time scale when conditions for energy balance were good (Calder 1994). The Tucson-wintering male's progressive storage followed a similar pattern, as if anticipating the cost of nocturnal temperature regulation (Fig. 3). Body mass upon arrival at the feeder perch increased linearly through the day ( $n = 38$ ,  $r = 0.92$ ,  $P < 0.001$ ), the regression on hour for 20 January being:

$$\text{mass} = 3.04 + 0.045 \times (\text{hour}).$$

This regression did not differ significantly when several days' data from intermittent monitoring were included (Calder 1994;  $n = 115$ ,  $r = 0.876$ ,  $P < 0.001$ ):

$$\text{mass} = 3.12 + 0.038 \times (\text{hour}).$$

These mass-gain rates of 4.5 and 3.8 mg/h exceeded what was observed in the Jalisco population, not surprising, given the unlimited artificial sucrose supply. This rate was at the high end of the range for maximum lipid deposition by migrant rufous hummingbirds (*Selasphorus rufus*), of 0.3 to 0.5 g/d (hourly 2.5–4.2 mg/h; Carpenter et al. 1983, Carpenter and Hixon 1988).

I determined meal sizes and total daily intake from the bird's body mass changes over an entire day (20 January). At dawn, he perched at the feeder often but briefly. Meal sizes were scant to unmeasurable, either because his digestive system was not ready for a larger intake of cold sucrose solution (dawn air 5.5 C), and/or because a higher priority went to re-establishment of his territorial claim. Meal size increased with time from 5 min after his first feeding, to average 0.15 g  $\pm$  0.10 SD ( $n = 37$ ) for the day, within the range of meal sizes of a territorial male Anna's Hummingbird using a feeder (Carpenter et al. 1991). Total intake for the day, 5.68 g of 35.4% sucrose solution (2.01 g sucrose), contained 33.1 kJ of energy, plus any net gain from feeding on aerial insects, which I observed in mid-day, unquantified. This was very close to the 1.98 g of sugar and 31.8 kJ of energy for Anna's Hummingbird in September, calculated from doubly-labelled water turnover (Powers and Nagy 1988). The thermoregulatory energy cost in their study would have been less in warmer weather (15.5 C minimum), reducing the potential for heat loss to 71% of what the Tucson broadtail faced ( $[40-15.5 \text{ C}]/[40-5.5 \text{ C}] = 0.71$ ). Their 4.48 g Anna's, however, weighed 31% more than this broad-tail, so would have required 21% more energy (metabolic scaling ( $1.31^{0.72} = 1.21$ ; Calder 1974). Thus size and seasonal differences tend to cancel.

On 20 January, the broad-tail gained body mass from 3.40 at daybreak to 3.80 g at dusk, representing 13.7 kJ of fat reserves, the most likely form of gain (see Calder 1994). In two final feedings, he increased in mass from 3.80 to 4.11 g (1705 h), then from 3.97 to 4.28 g (1717 h). As unconverted sucrose and water, 0.48 g of 35.4% sucrose would have added 2.7 kJ for a total of 16.4 kJ, or 1.19 kJ/h for the ensuing 13.8-h fast,

compared to a 1.06 kJ/h requirement calculated for his size and a body-air temperature difference of 40–5.5 C (Calder 1984: eqn. 8-15).

*Life history and annual cycle.*—Molt timing in the Tucson winterer was typical of a northern breeder wintering in Jalisco. Recaptured for examination on 2 February, his gorget was still dull-bronzy, as is seasonally characteristic of birds wintering in Jalisco (unpubl. data). Timing of flight feather replacement also coincided with that in Jalisco (Calder and Calder 1992). His 7th primaries were half-emerged, and the central rectrices (1, 2, 3) were emerging. By 6 February, his wings no longer whistled, so he had probably dropped the old sound-generating tenth primaries.

*Limitations.*—The range in minimum temperatures in this study was similar to that encountered by Broad-tailed Hummingbirds in montane summers of Colorado (Calder 1973, 1994). Therefore, in terms of temperature per se, the broad-tail could survive well to the north of its normal wintering range. Food supply thus seems more likely than temperature to be the factor that normally limits northern distribution of hummingbirds in winter. Watered landscaping and hummingbird feeders ease this limitation. Had the shorter days been a severe problem for adequate food intake, this bird would not have vacated his territory when an hour or more of daylight remained for feeding. His high rate of mass increase with artificial subsidy of sucrose solution provided enough energy to obviate any need for nocturnal hypothermia.

This male was last seen on 10 Apr. 1991 and was assumed to have migrated. He reappeared irregularly (band number confirmed 5 October) between 29 September and 15 December, but one or more in a series of seven Rufous Hummingbirds (29 September–3 April) may have preempted this winter territory. Interestingly, neither the seven Rufous nor the Calliope Hummingbirds returned for a second winter. Had they been disoriented or blown off course, or did they just shift wintering sites for some sensible reason?

Disorientation hardly seems an appropriate explanation for this extralimital wintering, given his demonstrated ability to return the next season. Furthermore, timing, essential for celestial navigation, was good on seasonal (e.g., molting) and daily (e.g., morning arrivals) scales. It would have been quite a coincidence for him to have been blown off-course to the same place in two consecutive years. Success in chasing away intruders suggests that flight and maneuverability were unimpaired. Escape from captivity was improbable. Daily mass gain rates equal to those of migratory refuelling (matching or exceeding other records, from feeders, flowers, and insects on a daily basis, make it seem rather unlikely that normal migration was canceled by inability to store energy. Thus his extralimital winter seems to have been a pioneering event, which though not necessarily of thoughtful purpose, may have been what expanded hummingbird distribution from tropical origins to 60°N and 54°S (Calder 1976, Greenewalt 1960). Broad-tails breed within 20 min flying time in the Santa Catalina Mountains north of the city, so elevational migration could have replaced the normal latitudinal migration.



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