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FEEDING ACTIVITIES OF THE ANNA'S HUMMINGBIRD AT SUBFREEZING TEMPERATURES

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In the past two decades or so, Anna's Hummingbirds (*Calypte anna*) have moved northward in the Pacific Northwest (US and Canada) to about 50°N latitude as year-round residents of urban areas. In this northern expansion of their range, winter exposes them to daylengths as short as 8 h, food limitations both in number of flowering species and in abundance, and periods of intense cold. Anna's Hummingbirds have been recorded during winter in Portland, Oregon, since late 1965 (Baldridge and Crowell, Audubon Field Notes 20:81–87, 1966); a first-year male was recorded between June and August, 1966, and subsequently the species has been seen in this area throughout most or all of the year (Zimmerman, Amer. Birds 27:827–835, 1973). With increased awareness of the presence of these hummingbirds during winter months, people have been maintaining hummingbird feeders year-round. We describe here feeding and resting activities of an Anna's Hummingbird near a feeder during low temperatures that may have approached the lethal point for thermoregulatory capacity in this species. Ambient temperatures during this period of cold approached the lowest ever recorded at a site of trochilid activity, and we have documented the longest profile of exceptionally low temperatures known to us within a hummingbird's home range.

On 26 December 1982, we placed a tube hummingbird feeder in our north-facing garden in Portland at 245 m elevation. Within three days, a male Anna's Hummingbird was attracted to the feeder, and one or more has visited daily ever since. Visitations peaked in July and August, when adults and immatures emptied the contents of the feeder (118 cc) daily. The sugar solution used in the feeder yielded approximately 1.7 kcal per cc, except when diluted in the tube by capillary action of surface water when it rained. A displacement air bubble, noticeable when a bird drank from the tube, approximated an intake of 0.5 cc, or 0.85 kcal, when the solution was at full strength. An 8-day continuous temperature recorder, connected to a thermocouple located at the same height as the feeder and 2 m away, provided a continuous profile of ambient temperature and was checked for accuracy at least four times a year.

A four-day period of cold, overcast weather, commencing 08:00 on 21 December 1983, broke previous records of low temperature for Portland on 23 and 24 December. In our garden, all but one hour of this period was below −4.4°C and ambient temperature dropped to −11.1°C (Fig. 1). When a hummingbird was present, we used a hand anemometer (Dwyer) to measure the winds that blew continuously from the east for the latter two days. These measurements revealed that the wind chill factor dropped the effective temperature to a low of −35°C on 23 December and to a low of −30°C on the following day while the bird was active.

Ambient temperature declined over the first two days, except during mid-day, at which times we saw hummingbirds at the feeder only between about noon and just before dusk at 16:30 (Fig. 1). This interval of sightings approximated the warmest segment of the subzero temperatures during daylight hours on each of these days and also on the third day, when the ambient temperature reached its nadir.

During the first two days, the hummingbirds usually came singly, and we observed no more than two, one of each sex, at a time. The birds were not banded, however, so we could not establish how many hummingbirds were visiting this feeder. When two were present simultaneously, they buzzed one another at the feeder in minor skirmishes. The male appeared to be the more frequent victor and also the more frequent visitor. Both sexes fed most actively just before dusk and ingested up to eight "bubbles-worth" of solution each in their final visits for the day. On the third day and until after the subsequent week, the visits were made only by a solitary male. He used the same twigs of a nearby rhododendron as perch sites between bouts of feeding on each visit, which suggested that it was the same individual each time.

Throughout the 4-day cold spell, the occasional precipitation was fine snow that did not accumulate and was driven horizontally when the east wind blew hard. The feeding and resting behavior of a hummingbird was essentially the same in routine, regardless of the extent of wind or precipitation. A visiting period lasted up to 10 min, during which an individual usually fed more than once and appeared to ingest 1–4 "bubbles-worth" of solution before departing. Between bouts of feeding in a visiting period, the bird usually perched 10–20 cm inside a rhododendron 3 m from the feeder. Even though its leaves were drooped and curled, this bush protected the birds from winds and periods of snow. Except for head movement and occasional preening, the bird was almost motionless while perched.

Ambient temperature rose to −1.67°C by 10:00 on 25 December and hovered between −2.78 and −1.67°C, with a wind chill of −15 to −10°C, until after dusk. Sleet and freezing rain fell throughout the day. On this morning, we placed a mechanic's light (40-watt bulb) in a rose trellis 10 m from the feeder, at the same height, and under the overhang of an eave. We first saw the male hummingbird at 14:30. After feeding and resting in the rhododendron several times, he flew to the trellis and perched there 30 cm from the light. Except for remaining in the garden and perching on the trellis, the routine of feeding activity was the same as on previous days. In the next two hours, he had about six bouts of feeding as sleet fell, returning to the protected trellis perch each time. By 15:30, when he was 15 cm from the light, we approached him, placing one bulb thermometer 15 cm from the light and within 5 cm of the bird, which remained on the perch, and another bulb thermometer 15 cm from the feeder. They registered 0.66°C and −2.30°C, respectively. From time to time, the

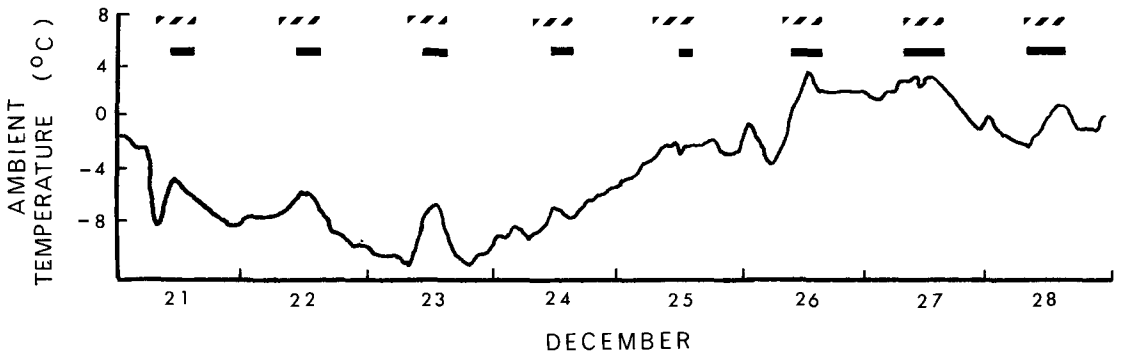

FIGURE 1. Feeding and resting activity of Anna's Hummingbird (*Calypte anna*) during a cold spell in Portland, Oregon. The hatched bars are the periods of daylight between sunrise and sunset, and the solid bars are the periods between first and last sightings of feeding and resting activities.

hummingbird was motionless when perched and may have been torpid for short intervals. Just before dark, he fed several times in rapid succession and disappeared.

Although the intense cold ended abruptly early the following day, the hummingbird arrived well before noon on each of the next three mornings, stayed almost all day by the light, and departed at dusk (Fig. 1). Even though ambient temperatures generally remained above freezing during daylight hours, the hummingbird appeared to be periodically torpid between flights to the feeder in the freezing rain. This daily routine ceased abruptly when a city-wide power failure, resulting from freezing rain, extinguished the light. From that time on, a male came to the garden several times a day to feed, perched for a few minutes on the trellis or elsewhere in the garden, and departed. Its feeding and perching behavior was essentially as it had been during the cold spell before the mechanic's light was introduced, except that at these warmer temperatures perching was not confined to the rhododendron and the bird commenced its visits well before noon.

Our brief observations document that the Anna's Hummingbird can thermoregulate effectively at ambient temperatures down to −8.9°C and at effective air temperatures down to −35°C created by wind chill. Although these small birds are exposed to a steep gradient of heat loss while active and able to feed, their energetic demands throughout a 16-h night without food and at even lower ambient temperatures would appear acute. The final intake of a bird at the feeder of up to eight "bubbles-worth" of sugar water at dusk would yield a maximum of 6.8 kcal for its major, and perhaps only, energy store for the night. This amount is only 1 kcal less than the average 24-h energy budget requirements calculated for this species in the mild climate of Berkeley, California (Pearson, Condor 56:317–322, 1954; MacMillen and Carpenter, Comp. Biochem. Physiol. A Comp. Physiol. 56:439–441, 1977).

The Andean Hummingbird (*Oreotrochilus estella*) is the nearest counterpart to the Portland residents of Anna's Hummingbird in terms of exposure to cold ambient temperatures in winter roosts (Carpenter, Univ. Calif. Publ. Zool. 106, 1976). The comparison may not be close, however, for the Andean Hummingbird, which regulates its body temperature at maximum energy savings while roosting at an average of 5°C in winter, weighs twice as much and apparently rarely, if ever, experiences ambient temperatures of 0°C or below. However, Anna's Hummingbirds in their northern urban habitats may circumvent their problem of exposure to life-threatening nocturnal air temperatures by roosting near external sources of heat around human habitations. Refuges, such as chimneys, lights, and heat pumps, may allow these birds to become torpid, or just sleep, at temperatures that minimize the risk of exhausting their energy budgets. Such ameliorating microhabitats may even assist them in surviving on days when at temperatures below −6.7°C their foraging time for caloric replenishment may be restricted to <4 h of daylight (Fig. 1).

Although we were unprepared to monitor the activities and energetics of the wild Anna's Hummingbirds in the record-breaking cold days of our observations, we have shown that they can be attracted to light/warmth under diurnal freezing conditions and can be approached closely. Thus, it should be feasible to record behavioral and physiological variables in unconfined birds by using remote and contact instrumentation. Such data may reveal the nature of the behavioral and physiological tactics, particularly under thermal stress of subfreezing conditions, that permit this species to extend its range of year-round residency to these northern latitudes.

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