SUN-ORIENTED DISPLAY OF THE ANNA'S HUMMINGBIRD

WILLIAM J. HAMILTON III

THE male Anna's Hummingbird (*Calypte anna*) executes a remarkable display which involves a nearly vertical power dive over the display object. A pinging noise made by the tail and a brilliant display of the iridescent purple-red feathers of the chin and forehead presumably enhance the display value of this performance. This display is given in all months of the year, but is most frequent from November to April, the breeding season of this California species. These hummingbirds are highly territorial (Pitelka, 1951*a*) and this display dive takes place only within the territorial confines.

The diving display proceeds as follows (Fig. 1):

1. The male climbs nearly vertically (A to B), in a hovering flight with the head bent downwards and the bill pointed towards the display object so that the male appears to be eyeing the display object as he ascends.
2. The male stops in midair (B), 100 to 150 feet above and to the side of the display object. At this point the bird hovers, making no appreciable lateral movement, so that his azimuth with respect to the display object is no longer adjustable.
3. Almost at once the male power dives, with a burst of wingbeats, each burst terminating with the wings held to the sides. Several power bursts take place in the downward dive which is made at an angle of perhaps 65 to 75 degrees from the horizontal (B to C).
4. The flight levels (C) several feet from the display object (E) and the male passes over this object almost horizontally.
5. At the moment the bird is over the display object (D) the tail is lowered, and by some manipulation, as yet poorly understood, the tail produces a sharp report.
6. At this point the flight is slowed, the bird veers upward, rises in a hook-shaped course 10 to 15 feet above and beyond the display object, and hovers at this position (F) momentarily.
7. He then moves upward again (F to B) to approximately the same position where the initial dive started and a new dive is executed. The number of dives is variable, from one to a dozen or more, frequently from three to eight.

When I first witnessed this display on 28 March 1956, in a residential area in Berkeley, California, I noticed that the dive oriented directly into the afternoon (1714–1755) sun. Between that date and December 1963, I have had opportunity to witness several hundred additional dives, all oriented toward the sun when the sun was directly visible to me. During periods of

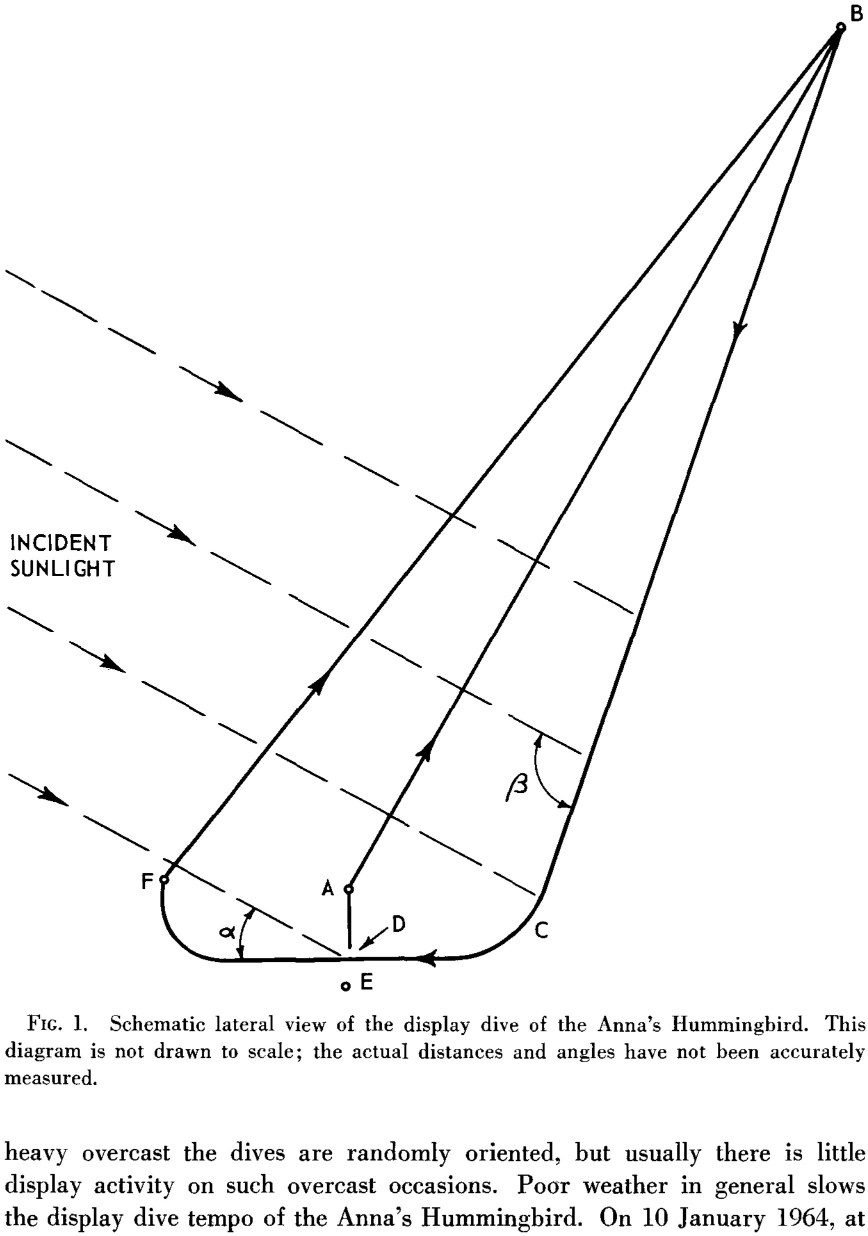

Fig. 1. Schematic lateral view of the display dive of the Anna's Hummingbird. This diagram is not drawn to scale; the actual distances and angles have not been accurately measured.

heavy overcast the dives are randomly oriented, but usually there is little display activity on such overcast occasions. Poor weather in general slows the display dive tempo of the Anna's Hummingbird. On 10 January 1964, at 1220, I was in the Japanese Tea Garden in Golden Gate Park in San Francisco. The day was almost completely overcast, the result of a low stratus formation. No clear shadows could be distinguished, but the location of the sun was clearly discernible. A male Anna's Hummingbird was heard displaying several times, and when I managed to locate him he dived so that the horizontal part of the flight was oriented almost directly *away from* the sun.

Display dives are usually directed at some fixed identifiable object, such as another hummingbird, male or female, or some other species of bird intruding into the territory such as the thrush, *Hylocichla guttata*, or even a man. Since this stimulus object triggers the dive, the dive has a double azimuthal orientation, being horizontally oriented with respect to the stimulus object and the sun. The sun orientation, therefore, must be made during the upward (A to B and F to B, Fig. 1) flight. There seems to be little if any azimuthal deviation during the downward dive. Loye Miller tells me that he has seen a horizontally kinked course during the dive. It seems likely that such deviation of the course is made relative to the stimulus object rather than the sun. I have never seen a dive pass to the side of the stimulus object.

Occasionally no stimulus object is apparent. Pitelka (1942) suggests that these displays may be triggered by other singing or displaying males nearby. In these instances the dive passes over the singing post, and for our purposes in evaluating the directional component of the dive the singing post may be considered the display object.

While the downward flight is usually quite precisely oriented to pass directly over the display object, it is not always oriented absolutely into the sun. If the performance is viewed from the side, as is usually the case, one can only say that the dive is oriented in the general direction of the sun. On 14 January 1962, I heard two pings from dives outside my office window of the California Academy of Sciences in Golden Gate Park, San Francisco. From "field" notes taken then:

"The male climbed away from the sun with respect to the female. During dives 3 through 7 (the first 2 were heard only) I could accurately line up his position over the cornice of the building. The third dive passed directly over the female and slightly to the left of the sun. Each successive dive through the seventh started slightly further counterclockwise with respect to the female, so that the seventh dive was oriented about ten degrees to the right of the sun. The eighth through the eleventh dives started behind the building at a point I could not see, but they apparently continued the circling trend. Each of these nine dives went directly over the female with the usual ping."

On 20 and 21 April 1956, Jay Schnell and I placed a mounted male and female Anna's Hummingbird in the territory of a male Anna's Hummingbird at Arlington, in the hills above Berkeley, California. On several occasions this male dived at the wired male while I held the attachment wire in my hand. In this circumstance the orientation of the dive was easily determined, and the effect of the dive could be more fully appreciated from this vantage point. The effect is one of a tiny ember, suddenly descending upon the observer, growing in brilliance and dimension as it approaches, to burst with a pop as it passes over the display object. If the object is not alert to this hummingbird prior to the first dive, there is little likelihood that a series of these performances could be ignored.

The Allen's (*Selasphorus sasin*) and Rufous (*Selasphorus rufus*) Hummingbirds, which have similar display dives, have no consistent orientation with respect to the sun. In the course of mounting to the point of initiation of the dive these birds fly upward, with the bill forward. This contrasts with the helicopter-like rise of the Anna's Hummingbird from A to B or F to B (Fig. 1) which is made with the head continuously oriented towards the display object. At point B these *Selasphorus* species make a sharp sweeping turn and plunge. These species are more erratic in the course of the downward descent, with frequent sharp turns in the flight course. These comparisons lend support to the suggestion that in the Anna's Hummingbird the orientation components are resolved in the course of the upward movement.

The significance of this sun orientation of the display would seem to be enhancement of the reflecting value of the iridescent gorget feather tips during this display. Greenewalt (1960) has pointed out that the effectiveness of iridescence depends upon: (1) the position of the observer with respect to the iridescent plumage and the sun; (2) the angle of placement of the microscopic components of the feathers; and (3) the position of the feathers on the body. The latter two factors will modify the first only to the extent that they will influence how critical the displayer–observer–sun relationship must be. Irrespective of the latter two, however, the display value of the performance will be enhanced by sunward orientation.

Among hummingbirds, analysis of the orientation of display dives suggests possible insight into ecological and evolutionary relationships. The maximal selective premium in terms of display value would be derived when the angle between the horizontal component of the dive and the direction of incident sunlight (angle α, Fig. 1) were closest to 0°. A zero value will be most closely approximated when (1) the breeding area is farthest from the equator, and (2) the season of display is closest to the winter solstice (21 December). Since the Anna's Hummingbird display falls in the winter months (Pitelka, 1951*a*, 1951*b*), the second requirement is near the maximal potential value for this species. The latitude of the breeding area of the Anna's Hummingbird, at 30–40° north, is well north of the breeding range of most hummingbird species.

These considerations do not, of course, explain the role of the vertical component (B to C) of these dives. For maximum reflection value the angle β in Fig. 1 would have to reach 0 as well, and random movements in and about the display object would improve upon the approximate observed values for this component. Presumably then this aspect of the dive functions to generate with the aid of gravity, sufficient speed to make possible the ping which is made over the display object and is not related to display of the iridescent plumage. The actual mechanism by which the tail sound is produced has not been investigated.

It is possible that display dives, especially those which are sun oriented, may have opportunity to develop only in very open areas such as the coastal vegetative complex of California where the Anna's Hummingbird breeds. Especially in tropical understory vegetation these displays would be unlikely to develop. These considerations suggest that the Anna's Hummingbird, a resident species in California, has been in this region for a considerable period of geologic time, probably without recent gene flow to other populations or areas. At the present time there is little avenue for such gene flow; the species is almost strictly limited to California, but a certain level of hybridization with related species persists (Banks and Johnson, 1961).

Skutch (1940*a*) has distinguished two basically different types of display among hummingbirds, "dynamic" and "static." The dynamic type is exemplified by the Anna's Hummingbird display dive described here. In addition, it is characteristic of the Broad-tailed Hummingbird (*Selasphorus platycercus*) (Skutch, 1940*a*), the Black-chinned Hummingbird (*Archilochus alexandri*), Costa's Hummingbird (*Calypte costae*), the Rufous Hummingbird (*Selasphorus rufus*), Allen's Hummingbird (*Selasphorus sasin*), the Calliope Hummingbird (*Stellula calliope*) (Banks and Johnson, 1961), and the Ruby-throated Hummingbird (*Archilochus colubris*) (Pitelka, 1942), the most northerly representatives of the hummingbirds. Central American species such as the Reiffer's Hummingbird (*Amazilia tzacatl*), White-eared Hummingbird (*Hylocharis leucotis*), and Heloise's Hummingbird (*Atthis heliosa*) do not have prominent display dives but confine their display energy to singing and gorget flashing at display posts, the static display type (Skutch, 1940*a*, 1940*b*).

Experimental evidence quite clearly demonstrates that the oriented migration performance of caged Starlings (*Sturnus vulgaris*) is based upon the sun (Kramer, 1956). When the sun is behind clouds below the artificial horizon of the apparatus which tests the orientation ability of Blue-winged Teal (*Anas discors*), orientation fails (Hamilton, 1962). The sun-oriented display reported here, however, apparently breaks down with moderate levels of overcast under conditions when the migratory orientation would persist. It seems possible, therefore, that the display orientation performance may be based upon shadows. Certainly shadows could provide adequate cues since the stimulus object is invariably elevated, either in a bush or tree, and the observed orientation could be achieved by lining up along the extension of the shadow of the stimulus object or its support. This hypothesis could be experimentally tested by shadow masking.

The orientation of bird displays with respect to the sun has received little attention. The Satin Bowerbird (*Ptilonorhynchus violaceus*) usually builds its display bower along a north–south axis and will correct the orientation of the bower if it is experimentally altered. Marshall (1954) suggests that "the utility of north–south orientation may be that very early each morning when energetic display begins, the male can keep the motionless female in view without staring straight into the rising sun. Likewise she can watch his flashing display without discomfort." However, at the season of display the sun rises in the northeast, so that bower orientation could be more appropriate with respect to Marshall's (op. cit.) suggestion, i.e., perpendicular to the northeast–southwest axis, the sun would apparently not enhance the display value of the male's iridescent plumage. This and the whole problem of the orientation of bird display with respect to the sun might be profitably studied on a comparative basis.

SUMMARY

The Anna's Hummingbird performs an aerial power dive display. The power dive passes over the display object and a sharp sound is made with the tail feathers. The bird then lofts high into the air to make repeated dives. The azimuthal component of this dive is always oriented into the sun when the sky is clear. This orientation enhances the display value of the iridescent plumage of the male with respect to the stimulus object.

Under overcast conditions the orientation of dives is no longer sun oriented. A single observation suggests that when bright shadows are lacking but the location of the sun is clear, orientation fails. This suggests the possibility that the orientation of the dive is based upon shadows.

A sun-oriented display is most likely to evolve in species which have iridescent plumage and breed at high latitudes or in the winter months. The Anna's Hummingbird meets all of these criteria and is, as far as is known, the only species of hummingbird which orients its display with respect to the sun.

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NEW LIFE MEMBER

Burt L. Monroe, Jr. of Baton Rouge, Louisiana has recently become a Life Member of the Wilson Ornithological Society. Mr. Monroe is a graduate of the University of Louisville and will be a candidate for the doctoral degree at Louisiana State University in June of 1965. Long known among ornithologists as a most enthusiatic organizer and participant in Christmas Bird Counts in several parts of the United States, he has recently turned his interest to tropical birds and is currently preparing a book on the birds of Honduras. In addition to this book Mr. Monroe has published numerous articles in *The Wilson Bulletin*, *The Auk*, and other publications. He is a member of the Cooper Ornithological Society, The Kentucky and Louisiana Ornithological Society, the Society of Systematic Zoologists, the Lepidopterists Society as well as the American Ornithologists' Union for whom he is currently serving as chairman of the membership committee. He is married and has as a principal hobby, aviation, for which he holds a commercial license. The picture shows Mr. Monroe examining specimens taken on a recent collecting trip to Africa.