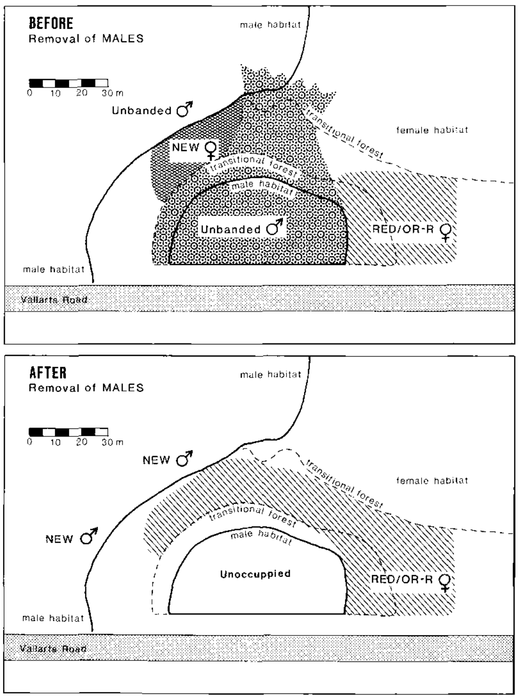

Fig. 2. Territorial configurations of male and female Hooded Warblers at site 2, located ca. 30 m west of the site in Fig. 1, before and after removal of two unbanded males. Other designations are the same as in Fig. 1.

1984, the former territory of the unbanded male (Fig. 2) remained unoccupied. Female red/orange remained in the crescent-shaped tintale habitat and did not use the vacant forest habitat. Also, she did not enter the forest habitat in response to playbacks of Hooded Warbler "chips" from within the forest habitat. Male white remained south of the road (Fig. 1) in the former territory of male dark blue, but had abandoned his original territory north of the road. The latter was occupied by an unbanded male.

We conclude that direct male exclusion of females from forest habitat is not a sufficient proximate explanation of habitat segregation between the sexes in Hooded Warblers. An alternative explanation is that the birds are simply sedentary and would not move into areas they did not occupy previously. However, our study was conducted at a time, just following migration, when territories were being occupied and boundaries were being defended actively, more so than is the case later in the season (J. F. Lynch pers. obs.). Also, both males and females (some of which may have been "floaters") were shown to move into areas vacated by our removal of males, but the original habitat segregation between the sexes was maintained nevertheless. Finally, the apparent reluctance of females to enter mature forest habitat, even when the latter was not defended by a male and was surrounded by female-occupied shrub habitat, is evidence that females and males "prefer" the different habitats in which we find them.

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A New Technique for Releasing Migrants from Orientation Cages

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In recent years, studies of orientation in migratory birds have proceeded along two largely independent routes. On the one hand, investigators taking advantage of Kramer's (1950) discovery have placed migrants in orientation cages of various designs and examined their behavior under a variety of conditions. On the other, fieldworkers have used radar and visual techniques to observe the orientation behavior of free-flying migrants under natural environmental conditions. The ability to systematically control potentially relevant variables has enabled those employing orientation cages to demonstrate a number

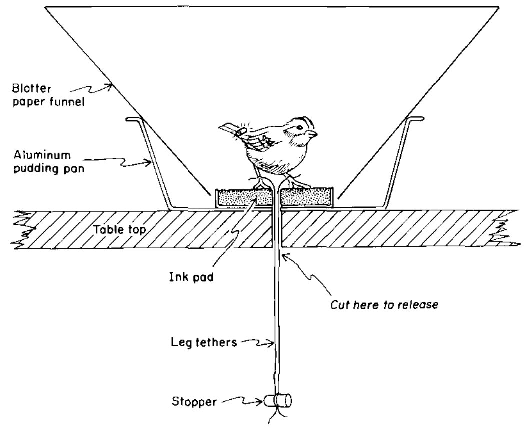

Fig. 1. Diagram of the apparatus used to release migrants. See text for a detailed description.

of important behavioral capabilities of migrants, viz., the sun, stars, and magnetic compasses. But studies of birds engaged in migration under natural conditions are necessary to reveal the full complexity of their behavior and to evaluate the relevance of experiments performed with captive birds (see Able and Cherry 1985). There has long been a need for techniques that combine the virtues of both approaches.

Demong and Emlen (1978) devised a technique in which birds are carried aloft in balloon-borne boxes equipped with a fused opening mechanism. At an altitude controlled by the fuse length, the box opens and the bird is dropped into the air. This technique was used successfully in several studies (Emlen and Demong 1978, Able 1978, Able et al. 1982, Bruderer pers. comm.), but it has a number of important disadvantages. First, birds released from the boxes are forced to fly. There is circumstantial evidence that many of the birds so released do initiate migratory flight, and criteria exist to attempt to discriminate those that do not, but one can never be certain that a bird dropped from a box into the night sky is actually migrating. Second, elaborate and expensive tracking equipment is required to obtain useful information on the released birds.

We have devised a technique that allows observation of night-migrating birds during the initial stages of migratory flight. Birds exhibiting *Zugunruhe* in orientation cages are released in a manner that allows them to initiate migration spontaneously. We have employed visual tracking, but other methods are feasible. The method allows the investigator to select individuals for release, to control the pretest experience of the bird, to manipulate conditions before release, and to obtain a record of the bird's hopping in the cage for comparison with its behavior in flight. Here we describe the technique in detail and present some first results from White-throated Sparrows (*Zonotrichia albicollis*) released under clear skies and in calm winds.

Experimental birds are placed in a modified version of the familiar Emlen funnel orientation cage (Emlen and Emlen 1966) (Fig. 1). The standard apparatus is modified as follows: (1) no covers are placed atop the cages, (2) the blotter-paper funnels must be taped to the pudding pans to prevent them from moving in the absence of the usual mass of the cage cover, and (3) a small (4-mm diameter) hole is made through the center of the ink pad and the bottom of the pan itself. Through this hole are threaded two thin tether lines (light-weight cotton thread, dissolving suture, or very thin monofilament) with pretied slip loops in the ends within the orientation cage. The other ends of the tethers extend down through the ink pad, pan bottom, and a corresponding hole in the platform on which the cages rest. A bird is placed in the apparatus by tightening one slip loop around each tarsometatarsus. While holding the now tethered bird in one hand, the tethers below the platform are grasped with the other hand. Free movement of the tether lines through the hole is checked and the length of tether above the ink pad is adjusted such that the bird can hop freely onto the sloping sides of the funnel, but is prevented from reaching its lip. When the proper length has been determined, a "stopper" (wad of tape, cotton stopper) is attached to the tethers immediately below the platform. This stopper prevents the bird from hopping too high and fluttering over the top of the funnel and at the same time provides enough mass to pull the tethers back down through the hole when the bird returns to the bottom of the cage. Once the bird is in place, the cages may be covered with opaque sheets while other birds are rigged. In practice, it pays to set up all the cage/tether combinations ahead of time so that the birds can be entered and the tethers adjusted rapidly.

To track the birds visually we attached small chemiluminescent lights to the bases of their tails. Cyalume light sticks (American Cyanimide Co.) are readily available in sporting-goods and hardware stores and can be opened and the two components separated. We applied this liquid directly to the plumage (rectrices) of birds, but absorption into the feathers and rapid deterioration of the light-emitting reaction in open air rendered this approach impractical. Using hypodermic syringes, the two components can be mixed in size 0 (20 × 5 mm) or smaller gelatin capsules that are then sealed by applying a small amount of water to the lip of the male portion of the capsule. Mixed in the proper proportions, these capsules produce adequate light to enable tracking for at least 3 h. The capsules were attached to the dorsal base of the bird's tail by clipping the upper tail coverts so as to expose the bases of the retrices, but not the uropygial gland. A small dab of livestock branding cement (AG-TEK Cement, Kane Enterprises, Sioux Falls, South Dakota) was used. In addition, we clipped

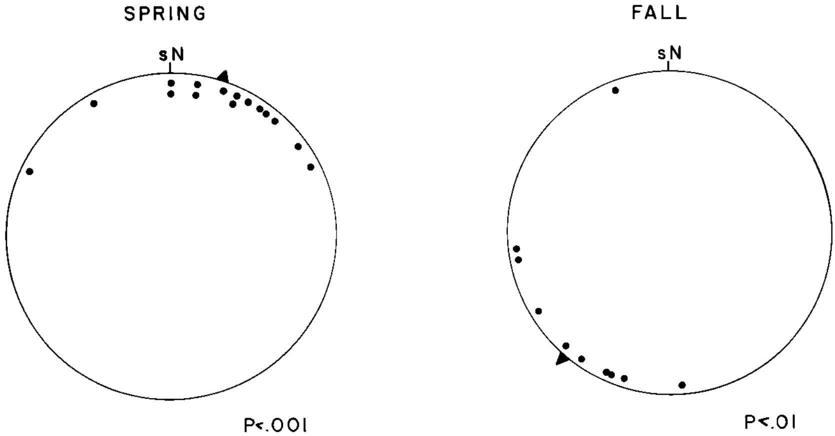

Fig. 2. Vanishing bearings of White-throated Sparrows released from orientation cages under clear skies and light winds. Vanishing bearings in spring (left) had a mean direction of 19° ($r = 0.862$, $n = 15$). The mean direction of vanishing bearings in autumn (right) was 227° ($r = 0.755$, $n = 10$). Significance levels are for the Rayleigh test. sN = stellar north.

the distal ±20 mm of the retrices to prevent the birds from "painting" the blotter-paper funnel with ink picked up by the tail tip.

During the experiment, the observer remains seated silently beneath the platform holding the cages. Once an actively hopping and fluttering bird is selected for release, the tethers are cut immediately below the platform surface (and thus above the stopper). If the cut is made when the bird is standing on the ink pad (i.e. no tension on the tethers), it will feel nothing. Although now free to fly from the funnel, the bird will not actually discover that it is loose until fluttering commences again. It was not unusual for several minutes to pass between cutting the tethers and flight initiation, and some birds ceased *Zugunruhe* and went to sleep after the tethers were cut, never taking flight although completely unrestrained.

Once a bird has taken flight from the cage, we observed its behavior visually using 10 × 50 binoculars or a night vision scope (Javelin Model 226, Javelin Electronics Div., Los Angeles, California). This permits a subjective description of its flight behavior, timing of the interval until disappearance, and measurement of the vanishing bearing. Vanishing bearings at considerably greater (but still unknown) distances could be obtained with radio transmitters. If it were possible to pick up the birds with radar, much more information could be obtained directly (track direction, altitude, ground speed) or calculated, knowing wind velocity at the flight altitude (heading direction, airspeed), but doing so consistently would be difficult.

Using these procedures, we tested White-throated Sparrows in spring (1982, 1984, 1985) and fall (1984, 1985) near Berne, Albany Co., New York. The birds, captured nearby while on migration, were placed in cages during the period between sunset and the first appearance of stars. The translucent plastic covers were removed no later than the end of Civil Twilight, but no birds were released until about 1 h later. Birds that took off when trees and shrubs were still visible in silhouette were more likely to land nearby. All tests were conducted on clear, calm nights with no more than a first-quarter moon. Standard methods of circular statistics (Batschelet 1981) were used to analyze directional data.

Of the 113 White-throated Sparrows placed in the release cages, the proportion showing nocturnal activity sufficient to warrant release varied greatly from night to night (20–80%), but averaged 55% (SD = 24%). Because we attempted to use highly motivated birds and conducted our experiments under ideal weather conditions, it is unlikely that the release percentage will average much more than this, at least for White-throated Sparrows. Some individuals ceased hopping shortly after release and never initiated flight. Among those that took flight, 44% (SD = 27%) flew until out of sight with our optical equipment, usually climbing more or less continuously. This proportion was also variable from night to night (0–100%). The remainder flew only a short distance after exiting the funnels and landed in nearby bushes or trees. As monitored by their light capsules, most of these birds remained *in situ* for the duration of our tests (sometimes up to 3 h). Because of the strong tendency for birds either to land nearby or fly a considerable distance, it was easy to define operationally an individual that initiated migration as one that flew out of sight (analogous to a vanishing bearing in homing pigeon studies).

Most birds that initiated migration by our definition flew directly away from the release point. A few made broad zig-zags or curved gently, but only three circled at a considerable range, thus creating a parallax problem and potentially yielding vanishing bearings divergent from their true flight headings. With visual tracking it was impossible to determine the range at which the birds disappeared. The duration of individual flights ranged from 0.9 (when the bird was lost behind horizon trees) to 10 min ($\bar{x}$ = 4.0 ± 2.6 min). At a typical take-off airspeed of about 9 m/s (Demong and Emlen 1978, Able et al. 1982), the average released bird was thus observed over about 2 km of flight.

In spring the mean vanishing bearing of released birds was 19° ($r = 0.862$, Rayleigh $P < 0.001$), and in autumn it was 227° ($r = 0.755$, $P < 0.01$) (Fig. 2). These means correspond closely to the average track directions of free-flying migrants in this area (Able 1982, Bingman et al. 1982, unpubl. data). This, coupled with the highly clumped distributions of vanishing bearings, inspires confidence that the flights observed were reflective of a migratory motivation.

There seemed to be a reluctance on the birds' part to hop actively when tethered. Some individuals tested in both standard Emlen funnel cages and the tether design were more active in the former. Once a tethered bird commences hopping, it becomes a candidate for release. Thus, the basic procedure tends to select against the accumulation of a large record of activity in the cage. To some extent, this problem can be alleviated by testing birds in standard cages on one or more nights before using them in a release experiment. Not only was the cage orientation much more variable than the vanishing bearings, but there was rarely close correspondence between the two.

The technique is not intended to provide an alternative to the orientation cage or to studies of free-flying migrants. It does, however, combine some of the advantages of both approaches and thus provides a means of addressing questions about orientation that require integration of behavior on the ground before the initiation of migration with that of a free-flying bird. It is important to attempt this integration because it remains a largely untested assumption that what we observe in an orientation cage reflects precisely what the bird would do if it was engaging in actual migration.

Advantages of the technique.—(1) Initiation of flight is a direct product of *Zugunruhe* and is spontaneous. Unlike the balloon/box method (Demong and Emlen 1978), the birds are not forced to fly nor stimulated to do so by the investigators. (2) The technique enables a comparison of the direction selected in the cage before release (under conditions in which various orientation cues can be experimentally controlled or manipulated) with that chosen in free flight. (3) Birds kept under different environmental conditions can be tested for differences in motivation to migrate. Questions concerning the ecology and physiology of migration can be addressed. (4) Individuals can be selected for release on the basis of their levels of *Zugunruhe* in the orientation cage. (5) Birds not released for any reason and those that do not take off after release can be retained for future use.

Disadvantages of the technique.—(1) Vanishing bearings are the only quantitative data obtainable without radar tracking. If a bird makes large changes in flight direction, especially when near the disappearing range, the vanishing bearing will be a poor estimate of the bird's actual heading. (2) The distances that birds can be tracked visually are rather short. Two observations suggest that this is not a critical disadvantage. First, very few of the birds we have released performed large changes in direction after the first few seconds of flight. Second, long radar tracks of White-throated Sparrows released from balloon-borne boxes showed that the birds rarely changed direction after the first few seconds of flight (Emlen and Demong 1978). (3) The procedure is time-intensive, and it is difficult to achieve large sample sizes. We have found that 20 birds is about the maximum that can be set up by two people for a single test. Of these, not all will be active and some of those released will not yield usable data. (4) The technique can be used only when wind speeds near the ground are light.

Additional work will be required to resolve the inconsistencies between the vanishing bearings and the quality and direction of the birds' activity while in the orientation cages. The release technique itself produces reliable results and is uncomplicated and inexpensive. It provides a means of spanning the gap between controlled studies of birds in orientation cages and observation of the behavior of free-flying migrants.

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