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Individual Group Flight of European Starlings and Budgerigars in a Wind Tunnel Without a Horizon Reference

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INDIVIDUAL AND GROUP FLIGHT OF EUROPEAN STARLINGS AND BUDGERIGARS IN A WIND TUNNEL WITHOUT A HORIZON REFERENCE

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ABSTRACT

I studied the ability and willingness of European Starlings *(Sturnus vulgaris)* and Budgerigars (*Melopsittacus undulatus*) to fly under different lighting conditions in a wind tunnel. My observations indicate that these birds can fly under conditions that supply no visual reference points, but their flight ability is more proficient when some light is available. The addition of a single horizon line to dark conditions improved the birds' flight ability and willingness, as indicated by an increase in the number of birds that took flight after landing. When small flocks were flown in the wind tunnel there was contact between birds in all lighting conditions. The collisions did not cause major disruptions of flight, but the birds seemed to be limited by the small space of the flight chamber. I conclude that (a) mechanisms in addition to sight may influence flock structure and (b) lack of visual cues may affect the primary orientation of birds enough to cause behavioral effects.

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Preface

This thesis has been prepared in the manuscript format that is acceptable to the Graduate School of the University of Rhode Island. Appendices are included to provide supplemental information.

The manuscript and literature cited section were prepared following the format for The Auk. A bibliography for the entire thesis is included after the appendices.

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ABSTRACT.— I studied the ability and willingness of European Starlings *(Sturnus vulgaris*) to fly under different lighting conditions in a wind tunnel. My observations indicate that starlings can fly under conditions that supply no visual reference points, but their flight ability is more proficient when some light is available. The addition of a single horizon line to dark conditions improved the starlings' flight ability and willingness, as indicated by an increase in the number of birds that took flight after landing. When small flocks were flown in the wind tunnel there was contact between birds in all lighting conditions. The contact did not cause major disruptions of flight, but the birds seemed limited by the small space of the flight chamber. I conclude that (a) mechanisms in addition to sight may influence flock structure and (b) lack of visual cues may affect the primary orientation of birds enough to cause behavioral effects.

MANY SPECIES of birds do not restrict their flight activity to the daylight hours. Although some species seem to be specially adapted for nocturnal activity, (e.g. owls, oilbirds) they are not the only ones to fly at night. Many species that migrate long distances do so exclusively at night (Berthold 1993). Other, non-migratory species such as Budgerigars (*Melopsittacus undulatus*) and European Starlings (*Sturnus vulgaris*) will fly, even in large flocks, long after the sun has set (Eastwood 1967, Wyndham 1980). Nocturnal migration and flocking after dusk seem to occur under a variety of meteorological conditions including fog and heavy cloud cover (Evans 1972, Elkins

1983). These behaviors imply that visual references may not be necessary for at least some bird species to maintain straight and level flight.

Radar echoes have been used to follow the tracks of nocturnal migrants and facilitated the examination of the effects of meteorological conditions on flight behavior. Studies have correlated aspects of migratory behavior with meteorological factors including cloud cover (Eastwood 1967, Alerstam 1976, Elkins 1983 and Bruderer et al. 1995). However, there are factors that limit the ability of radar to examine the flight behavior of birds within clouds because it is difficult to assess the cloud conditions immediately surrounding the bird being tracked (Bruderer and Steidinger 1972). In addition, the position of the bird cannot always be pinpointed, only the volume of space that it currently occupies. Dense clouds can also disrupt the radar echo from a bird target.

Williams et al. (1972) followed the tracks of birds that appeared to be flying in conditions that might preclude the use of visual cues to maintain straight and level flight. The birds were flying at an altitude that placed them between two cloud layers at night. Although some tracks were straight, others descended and did not maintain constant headings. The authors suggest that the lack of visual cues caused the birds to be unaware of changes in wind direction, but it is equally plausible that the birds were unable to maintain straight and level flight regardless of the direction of the wind. That the birds were flying at all under these conditions suggests that some straight and level flight without obvious visual cues is possible. Alerstam and Ulfstrand (1974) report aberrations from typical migration patterns when fog reduced visibility over large areas. The avoidance of areas of fog was attributed to the inability to use ground landmarks to determine course, although the possibility of losing control of straight and level flight may be just as important a reason for avoiding fog. Unfortunately, the vertical extent of the fog was not known. Thus, it is uncertain whether the few birds that did fly in the foggy areas were within or above the fog.

Griffin (1972) acknowledged that evidence of flight within clouds was anecdotal and inconclusive. He used a tracking radar on nocturnal migrants under overcast conditions to examine the effect that those conditions had on the birds' ability to navigate. Although he ran into problems with certainty of cloud conditions at all times and precise location of birds, he was able to track some birds and compare their flight paths with the current meteorological conditions. Some of the tracks he obtained appeared to be straight and level, but others were so erratic that the total distance flown was more than twice the ground distance covered. Other tracks actually stopped and the bird seems to have remained within the resolution of the radar beam for up to twenty seconds. It was concluded that birds flying within clouds often deviated from straight flight more than those above the cloud layer. The cause of the deviations could not be distinguished as either loss of just a sense of compass direction or an inability to maintain straight and level flight.

Able (1982) also used a tracking radar to examine the behavior of nocturnal migrants under overcast conditions. He concluded that overcast did not result in any changes in flight behavior. However, he acknowledged that some degree of disorientation did occur when birds seemed to be flying within or between cloud layers. Unfortunately, no distinction was made between primary and secondary disorientation.

Williams and Teal (1973) blindfolded individuals of six species of birds [Song Sparrow (*Melospiza melodia*), White-throated Sparrow (*Zonotrichia albicollis*), Slatecolored Junco (*Junco hyemalis*), House Sparrow (*Passer domesticus*), Domestic Pigeon (*Columba livia*), and Herring Gull (*Larus argentatus*)] and observed their flight to examine their ability to maintain straight and level flight in the absence of visual cues. One out of every six birds tested tried to fly upside down and crashed, and one-third of the birds dropped immediately to the ground. Fluttering flight was more common than level flight and gliding flight was rare. The observation that some of the birds maintained level flight, gained altitude or glided does indicate that for a short time visual cues are not necessary for straight and level flight, but I question the generality of these findings. Only Herring Gulls (*Larus argentatus*) seemed to be little affected by the blindfolds and some exhibited normal flight. However, two of the gulls would not fly and had difficulty standing upright.

Hochbaum (1955) also examined the flight of blindfolded birds. He used three species of birds and blindfolded them with a paper mask. Only five percent of the birds were reported to be unable to maintain normal flight and the majority made gentle landings. The effectiveness of the masks seems uncertain as birds deprived of sight are unable to sense the proximity of the ground and make sprawled or tumbling landings (Beecher 1952).

Two types of orientation might be affected if visual cues are removed from a flying bird. The first is primary orientation which concerns the positioning of the organism in three-dimensional space with reference to a constant direction, such as the gravitational pull of the earth (Fraenkel and Gunn 1940). Superimposed upon this primary orientation is secondary orientation, which relates to the organism's ability to maintain a directional heading across the earth (Fraenkel and Gunn 1940). A bird deprived of visual cues might find it difficult to maintain a compass heading or heading toward the roost, but it might also experience a breakdown of primary orientation and be unable to maintain straight and level flight.

Primary or positional orientation has been studied relatively little, especially with respect to flying organisms (Jander 1975). Pigeons have been shown to utilize an intestinal rotation compensating reflex based upon stretch receptors located in the mesenteries (Delius and Vollrath 1973) and all vertebrates can use semicircular canals to counteract angular accelerations (Jander 1975). The role of vision and horizon references in maintaining primary orientation has not been established for many organisms (Jander 1975). Schöne (1984) divided the stabilizing systems that contribute to maintenance of primary orientation into optomotor mechanisms and inertial systems. The optomotor mechanisms rely on visual input and are therefore unable to contribute to primary orientation when visual cues are lacking. The inertial mechanisms, namely the semicircular canals, must be relied upon in circumstances where visual cues are absent. In humans, the inertial systems are often not adequate to maintain primary orientation when there is no visual input or confusing visual input. Slanted banks of clouds can cause a pilot to unknowingly fly in a bank (Bending 1959, Gillingham and Wolfe 1986). If no visual horizon reference is available and the pilot is flying without instrumentation, the ability to keep the plane straight and level will be lost almost immediately and a total loss of control and downward spiral or spin to the ground are usually the result (Spector 1967). Spatial disorientation can be classified as vertigo when the subject experiences a false sense of rotation with respect to the environment (Bending 1959).

The amount of time without visual cues that might be necessary to cause disorientation is quite small. Anderson (1983) pointed out that when airborne, an animal will be unable to sense moderate wind changes and be prone to drift if fixed reference points are not available. Furthermore, all of the sensory indicators that contribute to an organism's sense of the vertical are remembered only for seconds, not minutes (Anderson 1983). Without any visual reference points, all changes in pitch (tilting up or down of the anterior or posterior part of the body), roll (sideways tilting around the longitudinal axis) and yaw (left or right swaying around the vertical axis) must be sensed and adjustments must be made to maintain a correct estimate of the vertical. Any error in this process will lead to an incorrect estimation of the direction of vertical and contribute to disorientation.

Birds that fly in flocks at night face the problem of collision avoidance, as well as maintenance of primary and secondary orientation. However Emlen (1952) noted that darkness was often associated with increased flocking in many species. During daylight flight these flocks can exhibit highly synchronous maneuvers in which every member of a flock may appear to execute the maneuver simultaneously. The mechanism for such rapid group actions is debated (Davis 1980, Potts 1984). This synchronous behavior may depend largely upon the acuity of avian vision and at night the distances between individuals in a flock are larger (Zuur 1984), but some of this maneuvering in tight formation is seen in low light conditions (Wyndham 1981).

My study utilized a wind-tunnel to examine the flight behavior of European Starlings under four different lighting conditions, ranging from normal indoor lighting to darkness. The birds were flown individually to determine their ability to maintain straight and level flight with and without visual cues. In addition, small flocks of three birds were flown under the same lighting conditions to examine the effect that reduced visibility might have on maintaining a flock.

Materials and Methods

Starlings were captured from a wild population by mist netting under a nocturnal roost site. All birds were kept at the Animal Care Facility at Brown University and cared for by facilities personnel. When the experiment was completed, the animals remained at Brown University for participation in future, non-related studies. All work was approved by the Institutional Animal Care and Use Committees at the University of Rhode Island and Brown University. Although the population from which these birds were taken is not migratory, it does fly in large flocks after sunset (R. Moyle, pers. obs.).

Wind tunnel design and bird selection.—The wind tunnel used in the experiments (Fig. 1) is located at Brown University. The working section of the wind tunnel measured 0.91 m (length) X 0.58 m (height) X 0.58 m (width) and was constructed of clear Plexiglas®. A 17 cm hole, 0.71 m from the front of the flight chamber along the left wall was used to insert animals into the flight chamber before each trial and extract them immediately after each trial. This hole was closed with a Plexiglas® disk that lay flush with the inside wall of the flight chamber during all trials.

A DC battery-powered fan in the exhaust section of the tunnel generated air flow. At the intake portion of the tunnel, there was a contraction portion (contraction ratio 2.19) that led to a 10 cm segment of honeycomb mesh (0.63 cm mesh) that also served as the front wall of the flight area.

The contraction portion and the honeycomb mesh reduce turbulence in the flight area. Turbulence levels in the flight chamber of this tunnel were measured at 3-5% using a hot-wire anemometer (Biewener et al. 1992). These turbulence levels are well within the ranges produced by other tunnels used in animal flight studies (Tucker and Parrot 1970, Hudson and Bernstein 1983, Rothe and Natchigall 1987).

Before any experimental trials began, the birds were acclimated to the wind tunnel. Birds that did not orient themselves correctly in the airstream and show some flight ability in the first week were removed from consideration. The remaining individuals were flown twice a day, three or four times a week until improvement in flight seemed to plateau. This plateau was achieved within five weeks when birds were flown on a regular schedule. During this training period, birds were encouraged to fly for extended periods by placing a small cage with conspecifics in it on top of the wind tunnel, within view of the flying bird. At this point, birds that consistently flew for at least 2 min (4 individuals) were assigned to the experimental group. This experiment was designed to test whether or not birds have the ability to fly with no visual cues, not to assess the population mean ability or range in abilities; consequently, a random sampling of the field population was not made. Preliminary work with Budgerigars influenced the decision to only use four starlings for the study group (Appendix A). When a large number of Budgerigars were flown separately in the wind tunnel, the differences in acclimation to the tunnel conditions caused high variances in data collected and precluded any statistical analysis. Any difference in acclimation to the wind tunnel in the experimental group could cause differences in behavior in the different light regimes to be hidden or exaggerated. Approximately half of all birds tested in the wind tunnel were able to adjust to the conditions and demonstrate some flight. However, the proportion that were eventually able to fly regularly for more that a minute was around 1 out of 6.

Experimental design.—Four different light regimes were used and were repeated for trials using single birds and trials with small flocks (3 birds). Wind speed in the flight chamber was between 12.5 ms^{-1} and 14 ms^{-1} for all trials. Each trial lasted for 60 s. Between 0 s and 5 s, the birds were introduced and hand released into the flight chamber. The birds chosen for the trials had consistently flown upon introduction into the wind tunnel and continued to do so in the experimental trials. Between 10 s and 15 s, any lighting changes that were due to occur in that trial were implemented. From 15 s until the end of the trial at 60 s, light conditions remained constant. At 60 s, any lighting changes were reversed and the birds were extracted from the wind tunnel.

Light level measurements were made with a Gossen Luna-Pro incident light meter. All trials were made with the room lights extinguished. Light for the experimental trials was provided by a single 120 v photographic flood lamp aimed at the ceiling. This produced 1400 lux (lx) in the flight chamber, approximately the same as provided by fluorescent ceiling lights. This provided moderate, but diffuse lighting in the entire wind tunnel laboratory. The front and back screens of the flight chamber were easily visible, as were all details in the laboratory. The four light regimes were:

"Light" Light levels were 1400 lx and remained constant throughout the trial. These trials should indicate the flight ability and behavior in the wind tunnel with no adverse lighting conditions.

"Dim" Between 10 s and 15 s, of each trial, the flood lamp was gradually dimmed from 1400lx at 10 s to 1.2 lx by 15 s. This provided diffuse and very dim light in the laboratory. When thus illuminated, the front and back ends of the flight chamber could be distinguished by a human observer as being darker than the walls. In the laboratory, shapes could be distinguished but no details. These trials were performed to determine if any change in flight ability, willingness or behavior was caused by a decrease in light level but not by the resultant light level.

"Dark" Between 10 s and 15 s of each trial in this condition, the light was gradually extinguished. To block any extraneous light, black electrical tape and tar paper were used to cover any light sources in the room. Under these circumstances, there was < .085 lx (the limit of the light meter's sensitivity) in the flight chamber and no light or shapes were visible in the room to a human observer dark-adapted for two minutes.

"Reference" These trials were exactly the same as described for "Dark" except that a luminescent strip 0.58 m long and 4 mm wide was placed across the wind tunnel midway up the front screen. The luminescent strip consisted of a length of adhesive luminescent material cut from an "exit" sign. The material was attached to a thin metal strip 4 mm wide. The metal strip was fastened to the front screen of the flight area. Twelve cm of the material was also placed at the same level at the front end of each side wall of the flight chamber. The luminescent material recharged when exposed to light, and in complete darkness remained visible to a human observer for over 2 min. The strips were visible but were not bright enough to illuminate anything else and provided a horizon reference inside the tunnel.

Changing the order of light regimes each day minimized any learning that might occur and preclude predicting any impending light change. Each bird participated in three trials per day and the order in which light regimes were presented to each bird was not repeated. The starlings would be unable to predict what would happen to the light levels until any change actually occurred. Each individual bird flew in each light regime three times alone and three times as a part of different flocks.

After all of the individual and flock trials were completed, each of the four birds was flown alone in the "reference" conditions with the 12 cm side strips of luminescent material removed. However, this time the horizon reference line was manually tilted from horizontal to approximately 20° from horizontal after a bird had begun flying in the wind tunnel and the lights had been extinguished for 10 s. If the birds were relying on the visible horizon reference for maintaining level flight, this shift might cause some change in flight behavior, whereas if the birds relied on any other source for maintaining primary orientation, there should be no change in flight pattern.

All of the trials were recorded with an infrared (IR) sensitive video camera and lighting system. One infrared flood lamp was placed on the left side of the wind tunnel slightly behind the flight chamber and approximately two meters from the tunnel. The lamp consisted of an infrared heat lamp inside of a metal box. The open end of the box was covered with a sheet of infrared filter material. The lamp was covered with tar paper to prevent light leaks around the seams. A dim red glow was visible at the front of the lamp but was removed by the addition of an additional IR filter in front of the lamp. The video camera used was a Panasonic WV-CD20 CCTV camera and was attached to a video recorder and monitor for playback sessions. The monitor was not used during any trials because of the light it produced. The images from the infrared sensitive camera were recorded on VHS video tape.

From the tapes of the trials, the time from introduction into the tunnel until each bird first landed was determined as well as the total time in flight. Total time of flight included any secondary flights after the initial landing. In trials using small flocks, the sample unit was individual birds, not the entire flock. The number of times each bird took off during each trial was also recorded. Finally, the method of alighting was characterized as (1) a controlled landing, (2)a crash or (3) a landing caused by the bird drifting into one of the walls, but with no evidence of a loss of primary orientation.

The difference between a crash and a landing in a wind tunnel is quite pronounced, as any major loss of control in flight results in the bird being immediately swept to the back of the tunnel and forced against the back screen. Contact with a wall may cause some disruption of normal flight rhythm and even a hasty landing, but to have been labeled a crash, the bird must have demonstrated a total loss of straight and level flight not caused by contact with a wall. In the experimental trials, the birds had no externally applied stimuli, such as electrically charged screens (Rothe and Natchigall 1987), to induce them to remain flying. The willingness to fly was indicated by the length of flight in addition to the number of reflights and the number of controlled landings. The ability to fly was indicated by the length of flights and the number of crashes. Long flights indicated a willingness and ability to fly under the condition, and the method of landing and number of reflights suggests the cause of the cessation of flight.

One-way repeated measures analysis of variance (ANOVA) was used to test for significant differences in mean total flight times between lighting regimes and between single birds and flocks. When statistically significant differences were found among treatment groups, a multiple comparison procedure (Student-Newman-Keuls method) was used to isolate the groups that differed from the others. Repeated measures ANOVA's on ranks were used when the data to be analyzed were not normally distributed.

RESULTS

Individual flight performance.—When flown individually, all of the birds used in the experiment flew for consistently long times in the "light" trials (Table 1). This might be expected as they were chosen for their ability to fly well under these conditions. Only 2 of the birds alighted in some manner before the end of the trial and both of those were controlled landings in the second half of the trial (38 s and 57 s). Although there was some contact between the birds and the transparent walls of the tunnel, this contact seemed more like brushing than colliding. This contact never caused the bird to lose control or crash. Under "dim" conditions, a bird alighted before the end of the trial 4 of the 12 times. Although two of these landings occurred late in the trial, similar to the "light" trials, two of the landings occurred at 15 s and 17 s. The bird that landed after 17 s later took flight again in the same trial.

The birds responded much differently to the "dark" conditions than to both the "light" and "dim" conditions. The mean total flight time in the "dark" condition was significantly shorter than in either the "light" or "dim" conditions (Table 2). None of the birds flew for the duration of a trial, and half of the initial alightings occurred between 15 s and 20 s, just after the lights were fully extinguished. Although the results from the "dim" trials suggested that some landings might occur in response to a change in light levels (2 in the "dim" trials), the number that actually alighted immediately after the light change was three times higher in the "dark" trials (6). In addition none of the birds took off again after landing in the "dark" regime, further suggesting that the actual light level was the cause of the change, not the change of light levels. One landing in "dark" conditions was labeled a crash.

When the luminescent horizon reference was added to the wind tunnel, there was a suggestion of both an increased ability and willingness to fly. The mean total flight time was not significantly longer than under "dark" conditions (Table 2), but only 3 trials had initial landings between 15 s and 20 s. The biggest change in the flight behavior between the "dark" trials and the "reference" trials was the number of reflights. While none occurred in total darkness, 5 occurred when a horizon line was present. The increased number of takeoffs resulted in an increased number of total landings but only controlled landings, not drifts or crashes. Altough the flight time difference is not significant, under horizon reference conditions the birds flew somewhat longer (27.8 s vs 22.5 s, Table 2), took off in the dark, and landed under control more often. That flight performance was poorer than in the "light" and "dim" trials was suggested by the observation that none of the birds flew for the duration of the trial, and they flew for a significantly shorter mean total flight time (Table 2). The data from all of the single bird trials are listed in Appendix B.

The Budgerigars used in preliminary work were highly variable in their flight behavior and influenced the decision to only use four starlings in the experimental group. Budgerigars flying alone in the wind tunnel, under the same conditions as the starlings, showed some of the same patterns as the starlings (Table 3). Only the "light" and "dim" trials had birds flying for the entire trial, but birds did fly in the "dark" and "reference" conditions after the lighting changes had been completed. The pattern of reflights also resembles the results from the single starling trials with no reflights occurring in the "dark" conditions but seven occurring in the "reference" trials.

Flock flight performance.—The data for the starling flocking trials are summarized in Table 4. Appendix C lists all of the data from the flocking trials. The four starlings used in the trials were identified with a red, white, brown or green leg band (hereafter referred to as Red, White, Brown and Green). When three of the birds were flown together, they tended to flock in the front third of the tunnel. Typically within 10 s, one of thebirds was usually forced down and made a barely controlled landing. Because the bird was able to successfully land on the bottom without suffering a large backward displacement, the landings were not considered crashes, but they did appear to be the result of contact with the other two birds at the front of the tunnel. Of the 48 bird trials (4 light conditions x 4 trials per condition x 3 birds per trial) conducted with small flocks, 12 resulted in one bird landing within 10 s of the beginning of the trial. In 7 of these trials it was Green that landed and in the remaining 5 it was Brown. The only time Brown landed before 10 s had elapsed was when Green was not in the trial or when Green was in the trial but also landed. Seven of the twelve flock trials in which Green participated resulted in Green landing before any light changes were initiated. These birds were fully able and willing to fly as they were also used in the single bird trials and flew as well as the other individuals.

Although many reflights occurred in the flock trials, the majority of those (12/18) can be attributed to Green or Brown taking off again and being forced down, typically within 5 s. If the trials with initial landings before 10 s are removed, the mean total flight times more closely resemble those for single birds and there remains a significant difference between the “light” and “dim” conditions and the “dark” and “reference” conditions (Table 2).

When the mean total flight times for all of the light regimes were grouped together, there was a significant difference between the mean total time for single birds and for those in flocks [34.0 s vs 23.5 s (medians), Friedman RM ANOVA on ranks, $P < 0.01$]. However, total mean flight time for flocks adjusted to remove those individuals that landed within 10 s of the trial beginning was not significantly different from total mean flight time for single birds (35.7 s flocks vs 39.7 s singles, one way repeated measures ANOVA, $P = 0.268$). When each light regime was analyzed separately, mean total flight time for single birds and flocks was significantly different in the “reference” conditions (Table 5). Mean total flight times for the other three light regimes between single birds and birds in flocks were not significantly different.

When the horizon reference line was shifted away from vertical, the birds neither crashed nor maintained normal flight. Instead, two of the four birds immediately landed precariously on the metal rod holding the horizon reference line. The line only protruded 3-5 mm from the front screen but the birds were able to cling to it. Within 3 trials in which the horizon reference line was shifted, all four of the birds landed on the line when it was shifted away from horizontal. Because the trials were conducted in the dark and no personal night vision devices were used, the shifting of the line was implemented by the experimenter approximately ten seconds after the lights had been extinguished and without any knowledge as to whether the bird had landed or was still flying. The birds landed on the line during the first trial that they were in the air when the line was shifted.

DISCUSSION

The results of this experiment suggest that although birds have some ability to maintain straight and level flight in the absence of visual cues, they appear to be more reluctant to fly under conditions of low visibility than they are when visual cues are available. The flight times in the "dark" and "reference" conditions were significantly shorter than in both the "light" and "dim" conditions (Table 2). However, even in the "dark" conditions, birds flew after the lighting change was made and landings were either controlled or caused by drifting into a wall of the wind tunnel. The increase in controlled landings suggests some unwillingness to fly in dark conditions. The true extent of flight without visual cues was not seen as the birds that continued to fly in the "dark" conditions either landed under control or were limited by the confines of the flight tunnel and drifted into walls that they could no longer see. The change of light levels also seemed to have had an impact upon the birds' willingness to fly. In the single bird "dim" trials two birds landed within two seconds of the light change. Two thirds of the single bird "dim" trials resulted in the bird flying for the duration of the trial and one of the birds that landed just after the light change later took flight again. This indicates that the low light level was not causing the birds to land but the sudden changing of the light level was a factor.

Physiological constraints can have a large impact on the decisions made by a migrant (Klaassen 1996). If loss of primary orientation may result from flying without any visual cue, a migrant must decide between energetically costly alternatives. The most probable cause of a complete lack of horizon reference would be clouds or fog. When confronted with a weather system that might eliminate a horizon reference, the airborne bird could maintain its altitude and heading and risk losing primary orientation. This could result in a loss of potential energy in the form of a drop in altitude or more costly fluttering flight. To avoid this possibility, the bird could choose to alter it's course or climb to an unobscured altitude. These choices have potential energetic costs.

Some of the same conditions that can cause spatial disorientation, namely conflicting visual and vestibular information, are also able to induce motion sickness (Money 1970, Gillingham and Wolfe 1986). Motion sickness causes a number of physiological symptoms. The two most common are nausea and emesis. Emesis resulting from motion sickness has been documented in birds as well as in mammals and fish (Money 1970, Gillingham and Wolfe 1986, Ueno et al. 1988, Kucharczyk et al. 1991). Conflicting information from the eyes and semicircular canals also includes a total lack of input from the eyes. Most blindfolded humans become nauseous and vomit when exposed to angular acceleration (Money 1970). The possibility of motion sickness when flying under conditions that provide no visual cues for primary orientation cannot be discounted as another reason for the unwillingness to fly demonstrated in the "dark" conditions in this experiment.

If the need to maintain a visual horizon reference is vital to an organism adapted to flight, the visual system might reveal some mechanism for acquiring a horizon reference under partially obscured conditions. Pennycuick (1960) attributes a bird's ability to establish a horizon reference at night or between cloud layers to the presence of a horizontal ribbon of acute vision, due to a high concentration of cone cells, in the retina of some birds. This would only help in situations with a discernible horizon reference. It is unlikely that this region of the retina is sensitive enough to pick up a horizon line from within a cloud at night. In addition, this retinal structure has not been found in all birds (Pearson 1972).

While radar studies have documented birds flying on overcast nights (Evans 1972, Griffin 1972, Alerstam 1976, Able 1982, Bruderer et al. 1995), it is difficult to determine if the birds were actually flying in the cloud layer. It is also nearly impossible to determine the position of a bird's body or the energetic efficiency of a bird's flight. Changes of heading and altitude in response to cloud formations have been documented (Griffin 1972, Williams et al. 1972) but the reasons for the changes are uncertain. The rain or wind that often accompany clouds could be an equally valid reason to avoid them.

Piersma et al. (1990) lists an overcast sky as one of the proximate cues a bird uses for delaying the onset of migration. The reason given is that a view of the stars would not be present and that would hinder ability to orient in the correct direction. While that is undoubtedly true, the energetic and possible other costs of flight under such conditions might hinder primary orientation and contribute to a bird's reluctance to depart on an overcast evening.

The trials in which a small flock of birds flew under various light conditions may suggest something about coordination of movement in organized flocks. If the maintenance of position in a flock depended upon vision alone, I predict flight performance in a flock flying in darkness should be below that of a single bird flying in the same light regime. While that appeared to be the case, most of the early landings in flocks can be attributed to all of the birds attempting to fly in the front third of the wind tunnel and one of them being forced to land, even when in full room lighting. When all birds were returned to a temporary carrying cage between trials, there was always an aggressive struggle to use the water bowl first. Green was pushed off the dish by any other bird and was only able to drink when the others were done and no longer contested it. Brown was pushed off of the water bowl more often than not, but was more successful than Green. The dominance hierarchy apparent in the cage appeared to extend into their flight behavior as well.

Brown and Fedde (1993) showed that birds may be capable of measuring airspeed and the flow of air over their wings using mechanoreceptors in the wings. These same mechanoreceptors might be able to detect the changes in the air flow caused by another bird in flight nearby. In this experiment, the experimenter could feel the wingbeats of the birds on his hand when it was positioned up to 50 cm behind the bird in the wind tunnel. Receptors sensitive enough to judge windspeed and detect changes in the airflow over their wings might be able to sense another's wingbeats as far away as a human arm is able to sense them. Photogrammetric tests have shown that the nearest neighbor in a flock of starlings is most likely to be behind and below the reference bird (Major and Dill 1978). This is the position where the aerodynamic influence of the bird in front would be the strongest and the logical place for the positioning of a nearest neighbor if pressure or air flow sensors could be used to aid vision in maintaining flock structure.

The lowering of the feet that was noticed by Williams and Teal (1973) in their blindfolded birds even when the birds had gained altitude or achieved level flight was also seen in this experiment. In the "light" conditions in the wind tunnel this might be attributed to seeing an impending collision and compensating for it by fending off an obstacle, or lowering its center of gravity to gain stability. However, in darkness birds may either be able to sense obstacles by means other than vision or be lowering their center of gravity as a precautionary measure to aid in maintaining level flight if primary orientation becomes difficult. In the dark conditions in the wind tunnel, the birds may also have some memory of the tunnel's dimensions and be aware that there are walls nearby that they can no longer see.

The experimental situation used for these experiments departs from natural conditions in several respects. The wind tunnel supplies a relatively constant air flow with low turbulence that is likely to be uncommon in the field. In addition, the motor that causes the air flow provides a constant auditory reference point for the flying birds. However, if anything, these artifacts should have improved the starlings' ability to fly in the dark. The wind tunnel is also very unforgiving of any problems with maintaining straight and level flight. Any fluttering flight or disorientation immediately results in the starling being blown to the back screen. While this is useful in being able to detect any loss of orientation, the behavior while disoriented is unfortunately not seen as the bird is immediately swept from sight.

Although an infrared lamp was used to provide illumination for videography, there is no evidence of infrared sensitivity in the starling that would enable it to use "infrared vision" to maintain a visual horizon reference in the dark (Adler and Dalland 1959). It has been reported that the majority of bird species seem to have night vision that is no better than a human's and a visible spectrum about the same as the human eye (Griffin 1955).

The shifting of the horizon reference line suggested that the birds may have been using it as a reference line and did not see it as a perch until it was rotated while they were flying. The fact that the birds did not attempt to compensate for the tilting of the horizon reference suggests that although they might use it as a visual reference, they were able to determine that the line was tilting away from the vertical instead of believing that they were actually rolling in the opposite direction.

While flock structure in birds is undoubtedly maintained by visual contact between individuals, the maintenance of such flocks after dusk may be augmented by the birds' ability to sense the disturbance in the air caused by its nearest neighbors.

The possibility of primary disorientation at night and/or in clouds should be considered as a possible constraint on the timing and paths of migrating birds. The timing of roosting and the amount of flocking after dusk in birds like starlings may also be affected by limitations of primary orientation. While starlings do appear to have some ability to fly with no visual cues, they do not appear to be able to do so reliably. This may have some effect upon the birds' decision making process in initiating flight in conditions where the horizon might be obscured. This is not to say that a bird will never fly through a cloud, but rather that there may come a point where visual cues become infrequent enough to cause the bird to alter its flight behavior.

Table 1. Mean time to first alighting (± SE), mean total flight time (± SE), and totals for the number of reflights, landings, crashes and drifts for trials using individual starlings (n = 12). Numbers in parentheses indicate the number of birds that landed in some manner in that light regime. Some birds flew for the duration of a trial and are not included in the time of first alighting. An alighting was listed as a drift if caused by contact with one of the tunnel walls. An alighting was listed as a crash if straight and level flight was lost without any evidence of contact with a tunnel wall.

Light regime	Mean time to first alighting (s)	Mean total flight time (s)	Total number			
			Reflights	Land	Drift	Crash
Light	47.5 ± 9.50 (2)	57.9 ± 1.83	0	1	1	0
Dim	29.8 ± 9.03 (4)	50.8 ± 4.65	1	3	1	0
Dark	22.5 ± 2.10 (12)	22.5 ± 2.10	0	5	6	1
Reference	25.3 ± 2.35 (12)	27.8 ± 2.47	5	10	6	1

Table 2. Mean total flight times of individual and flocks of starlings under 4 light regimes, including reflights. Means underlined with same line not statistically different ($\alpha = 0.05$; Student-Newman-Keuls multiple comparison method). Flocks* indicates flock data adjusted to remove any trials in which the bird landed within 10 s of the trial beginning.

Group	Light regime			
	Light	Dim	Dark	Reference
Singles	57.9	50.8	22.5	27.8
Flocks	43.5	39.5	19.2	17.2
Flocks*	49.0	59.3	22.3	18.1

Table 3. Mean total flight time (± SE), range in total flight time and total number of reflights, controlled landings, drifts and crashes for budgerigars flown individually.

Light regime (n)	Mean total flight time (s)	Range(s)	Total number			
			Reflights	Land	Drift	Crash
Light (12)	23.4 ± 5.05	7-60	7	16	1	1
Dim (12)	26.7 ± 4.93	8-60	16	24	0	2
Dark (16)	18.8 ± 1.92	8-32	0	6	8	2
Reference (24)	21.2 ± 1.34	7-41	7	22	4	3

Table 4. Mean time to first alighting (± SE), mean total flight time (± SE), and totals for the number of reflights, landings, crashes and drifts for trials using flocks (3 birds) of starlings (n = 4 flocks). Numbers in parenthesis indicate the number of birds that landed in some manner in that light regime. Some birds flew for the duration of a trial and are not included in the time of first alighting. An alighting was listed as a drift if caused by contact with one of the tunnel walls. An alighting was listed as a crash if straight and level flight was lost without any evidence of contact with a tunnel wall.

Light regime	Mean time to first landing (s)	Mean total flight time (s)	Total number			
			Reflights	Land	Drift	Crash
Light	7.3 ± 1.65 (4)	43.5 ± 7.10	4	6	1	0
Dim	12.8 ± 6.69 (6)	39.5 ± 7.25	8	8	1	2
Dark	16.3 ± 1.98 (12)	19.2 ± 2.93	6	17	1	0
Reference	17.2 ± 1.56 (12)	17.2 ± 1.56	0	10	0	2

Table 5. Mean total flight times for starlings and P-value from one way repeated measures ANOVA.

Light	Group		P
regime	Singles	Flocks	
Light	57.9	43.5	0.265
Dim	50.8	39.5	0.270
Dark	22.5	19.2	0.274
Reference	27.8	17.2	0.007

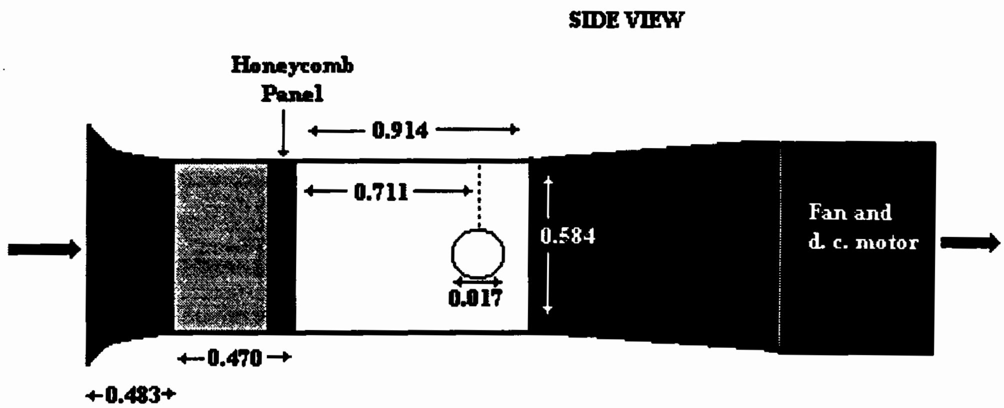

Fig. 1. Diagram of the wind tunnel from a side view. All measurements are in meters.

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Appendix A. - Methods and a summary of the results for trials using budgerigars.

Preliminary experiments were conducted prior to the mist netting of the starlings. The preliminary experiments were conducted on three starlings that were already being kept at Brown University for other experiments and four budgerigars. Parakeets were used because of their small size and ease of acquisition. The ones we used were on loan from a local breeder.

Although parakeets in the wild are not migratory, they are quite nomadic and often travel in large flocks. These flocks exhibit the same type of roosting behavior as is seen in starlings. The flocks will congregate at dusk and continue to fly in large numbers around the roost site long after sunset (Wyndham 1981, Kavanau 1987). For these reasons, they seemed like ideal subjects to add on as a second species in the wind tunnel trials.

Of the four original budgerigars, two became acclimated to the wind tunnel and would fly for more than a minute in full room lighting quite consistently. The other two budgerigars never acclimated and would never fly for more than 10 s. The starlings that were tested had been flown previously in the wind tunnel and flew consistently for a minute or more. It was decided that the budgerigars would form the first study group as they were available from the breeder immediately and when starlings began roosting in very large numbers in the winter months, they would be captured and added to the study.

Thirty budgerigars were obtained from the breeder and tested in the wind tunnel. The desired number of test subjects was 15 to allow for statistical strength. After several weeks of attempting to acclimate the birds to the wind tunnel conditions, the 15 best birds were chosen for the test group. The attempts to acclimate the budgerigars were similar to the methods described for the starlings in the main body of the paper. The remainder of the budgerigars were returned to the breeder. After one mortality and the return of two "breeder" birds to the local breeder, 12 birds remained for flight under the different lighting regimes. The experimental design for the budgerigars was the same as for the starlings except that the budgerigars were only to be flown once per light regime.

Birds chosen for the experimental group seemed to have acclimated to the wind tunnel differentially. Some individuals would fly for 5 min or more consistently while others would almost always land well before 1 min had passed. This variation in willingness or ability to fly under wind tunnel conditions might obscure any real differences in responses to different lighting situations. It was impossible to test a bird's reaction to decreased light levels if it was unable to establish a consistent level of performance in full light conditions.

Birds were only flown once each week for the next two months of the experiment. Before testing actually began, they were flown twice a day, three or four days a week for three weeks. This reacclimation period did not seem to return the birds even to their previous level of competence in the wind tunnel. The most consistent flyers still flew for at least a minute, but not for the several minutes that they had previously. The poorer flyers were at least as unreliable as before. It is uncertain whether it was the two months with very little flying time or simply the length of time since they were first exposed to the wind tunnel, but there definitely seemed to be a peaking or plateauing of their flight performance under wind tunnel conditions.

This peak and fall-off in flight performance is the opposite of what was seen in the starlings. The best flyers in the wind tunnel lab were birds that had been in captivity for months and had been exposed to wind tunnel flight the entire time. These birds would resume their long flights in the tunnel after several weeks with little or no flight time. The assumptions that had been made about the budgerigars on the basis of previous experience with starlings did not appear valid. Far fewer than half of the tested budgerigars ever became consistent flyers in the wind tunnel. When any birds were being acclimated to the wind tunnel for this experiment, a qualitative number system was used to rate their performance. Each flight that a bird made was assigned a number between one and three (including pluses and minuses). To receive a rating of one, a bird would have to fly for one minute or more with no assistance from the experimenter. If the bird was able to fly for periods of greater than ten seconds but less than a minute it would receive a two. A three would be assigned if the bird was unable to maintain any straight and level flight at all. The pluses and minuses were used to indicate that the birds performance was near the limit of performance covered by that number.

Only a bird that consistently received ones in its acclimation flights and had demonstrated that it was able to fly under wind tunnel conditions would be a suitable subject for the experiment. Because the sample size for the budgerigars was chosen purely for statistical purposes, birds that routinely scored below a one in their acclimation flights were included in the experimental group. The exact extent of the consequences of this action was not apparent until the trials were already underway.

Although twelve birds were scheduled to fly in each light condition, some of the birds ended up being flown more than once in the "dark" and "reference" conditions. The decision to fly some of the birds more than once in the "dark" and "reference" conditions was made after it became apparent that some of the budgerigars were not flying well in any lighting condition. Only one bird in each of the “light” and “dim” trials flew for the entire duration of the trial. Because of this, the difference in flight behavior that a change in lighting conditions might cause would be obscured by the poor results of some birds in all of the conditions. At this point it was decided that the budgerigar trials could still give some indication of the limits of the budgerigars’ flight in the “dark” and “reference” conditions. The most consistent flyers under “light” conditions were repeated in the “dark” and “reference” conditions.

Even when the best birds were flown more than once, the average total flight time in the “dark” conditions (18.6 s) was just longer than the time it took to make the lighting changes (15 s). Most notable in the data for the budgerigars is the number of reflights. In a pattern very similar to that seen later in the starlings, there were no reflights in the “dark” conditions but a total of seven in the “reference” conditions. The number of budgerigars that landed due to drifting into one of the walls is much lower in the “light” and “dim” trials (1 total) than that in the “dark” and “reference” trials (13 total). Even when taking into account the varying number of trials between light regimes the differences in the number of reflights and landings due to drifting into a wall are notable. The disparity in the number that landed due to drifting into a wall suggests that much of reduction in flight ability or willingness in the darker light regimes was due to an inability to determine the limits of the confined flight space in the dark and not necessarily an inability to actually fly straight and level under those conditions. The disparity in the number of reflights under “dark” and “reference” conditions suggests that the addition of a horizon reference line increases the birds’ willingness to fly in dark conditions.

The number of landings that were categorized as crashes was greater than that seen in the starling single bird trials. However, there is no trend in the number of crashes that occurred per light regime and may just be an indicator of the budgerigars poor flight performance in the wind tunnel in general.

With the additional number of trials added to the "dark" and "reference" trials, some extended flight was witnessed under these darkened conditions. In the "dark" conditions, one budgerigar flew for 32 s before landing due to drifting into the back screen of the flight chamber. Another budgerigar flew for 30 s before also drifting into the back screen. Two budgerigars flew for 28 s and 35 s before making controlled landings in the "reference" trials

The flock trials for the budgerigars were conducted in the same manner as the single bird trials. The total number of flocks flown is each trial was different than for the starlings, with "reference" trials having a greater number of flocks than any of the other light regimes. The generally poor flight performance of the budgerigars in the wind tunnel was exacerbated by the close proximity of the two other flying budgerigars. In all conditions, some birds landed before 10 s had elapsed in a trial. In addition, when one bird had landed the gregariousness of the budgerigars seemed to control their actions, as the other two budgerigars would usually land next to the first one. These group flights by the budgerigars were also marked by a large quantity of calling by the birds in the wind tunnel, with those in the holding cage outside of the wind tunnel invariably joining in.

Appendix B. - Individual starling trials data

Table 6. Starling single bird trials in the "light" condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/9/96	Brown	--	60 s				
2	4/9/96	White	--	60 s				
3	4/9/96	Red	38 s	38 s			1	
4	4/9/96	Green	--	60 s				
5	4/17/96	Red	--	60 s				
6	4/17/96	Brown	--	60 s				
7	4/17/96	Green	57 s	57 s		1		
8	4/17/96	White	--	60 s				
9	4/18/96	Red	--	60 s				
10	4/18/96	White	--	60 s				
11	4/18/96	Brown	--	60 s				
12	4/18/96	Green	--	60 s				

Table 7. Starling single bird trials in the "dim" condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/9/96	Red	--	60 s				
2	4/9/96	Brown	33 s	33 s			1	
3	4/9/96	White	--	60 s				
4	4/9/96	Green	--	60 s				
5	4/11/96	Green	17 s	27 s	1	1		
6	4/11/96	White	--	60 s				
7	4/11/96	Red	--	60 s				
8	4/11/96	Brown	15 s	15 s		1		
9	4/18/96	Green	--	60 s				
10	4/18/96	Red	--	60 s				
11	4/18/96	White	--	60 s				
12	4/18/96	Brown	54 s	54 s		1		

Table 8. Starling single bird trials in the "dark" condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/9/96	White	35 s	35 s		1		
2	4/9/96	Red	36 s	36 s		1		
3	4/9/96	Green	21 s	21 s			1	
4	4/9/96	Brown	19 s	19 s			1	
5	4/11/96	Brown	15 s	15 s			1	
6	4/11/96	White	18 s	18 s		1		
7	4/11/96	Green	21 s	21 s			1	
8	4/11/96	Red	31 s	31 s		1		
9	4/17/96	Brown	17 s	17 s			1	
10	4/17/96	Red	19 s	19 s			1	
11	4/17/96	White	17 s	17 s		1		
12	4/17/96	Green	20 s	20 s				1

Table 9. Starling single bird trials in the "reference" condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/9/96	White	32 s	32 s		1		
2	4/9/96	Red	39 s	39 s		1		
3	4/11/96	Green	22 s	28 s	1		2	
4	4/11/96	Brown	17 s	17 s			1	
5	4/11/96	Red	39 s	39 s		1		
6	4/17/96	Green	30 s	30 s			1	
7	4/17/96	Brown	15 s	15 s		1		
8	4/17/96	White	17 s	20 s	1	2		
9	4/17/96	Red	24 s	24 s			1	
10	4/18/96	White	25 s	38 s	2	2	1	
11	4/18/96	Green	24 s	31 s	1	1		1
12	4/18/96	Brown	20 s	20 s			1	

Appendix C. - Starling flocking trials data.

Table 10. Starling flock trials in the “light” condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/23/96	Brown	5 s	5 s			1	
	4/23/96	White	--	60 s				
	4/23/96	Red	--	60 s				
2	4/24/96	White	--	60 s				
	4/24/96	Brown	--	60 s				
	4/24/96	Green	5 s	5 s		1		
3	4/25/96	Red	--	60 s				
	4/25/96	Brown	12 s	17 s	2	3		
	4/25/96	Green	--	60 s				
4	4/25/96	Green	7 s	15 s	2	3		
	4/25/96	Red	--	60 s				
	4/25/96	White	--	60 s				

Table 11. Starling flock trials in the "dim" condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/23/96	Green	10 s	14 s	1	1		1
	4/23/96	Brown	5 s	5 s		1		
	4/23/96	White	--	60 s				
2	4/24/96	Brown	46 s	58 s	1	1		
	4/24/96	Green	4 s	12 s	2	1		1
	4/24/96	Red	--	60 s				
3	4/24/96	Brown	7 s	10 s	1	1	1	
	4/24/96	White	--	60 s				
	4/24/96	Red	--	60 s				
4	4/25/96	Red	--	60 s				
	4/25/96	White	--	60 s				
	4/25/96	Green	5 s	15 s	3	3		

Table 12. Starling flock trials in the "dark" condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/23/96	White	22s	22 s			1	
	4/23/96	Brown	24 s	24 s		1		
	4/23/96	Green	18 s	18 s		1		
2	4/23/96	Brown	5 s	5 s		1		
	4/23/96	White	18 s	23 s	1	2		
	4/23/96	Red	18 s	39 s	2	3		
3	4/24/96	Green	5 s	5 s		1		
	4/24/96	Red	22 s	30 s	3	4		
	4/24/96	White	24 s	24 s		1		
4	4/25/96	Green	8 s	8 s		1		
	4/25/96	Brown	15 s	15 s		1		
	4/25/96	Red	17 s	17 s		1		

Table 13. Starling flock trials in the "reference" condition. -- indicates that the bird did not land at any point during that trial

Trial	Date	Bird	Time to 1st landing	Total flight time	Reflights	Land	Drift	Crash
1	4/23/96	Red	26 s	26 s		1		
	4/23/96	Green	19 s	19 s		1		
	4/23/96	Brown	5 s	5 s				1
2	4/24/96	Red	20 s	20 s		1		
	4/24/96	White	18 s	18 s		1		
	4/24/96	Green	13 s	13 s		1		
3	4/25/96	White	20 s	20 s		1		
	4/25/96	Brown	12 s	12 s		1		
	4/25/96	Green	15 s	15 s		1		
4	4/25/96	Brown	17 s	17 s		1		
	4/25/96	White	19 s	19 s		1		
	4/25/96	Red	22 s	22 s				1

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