1908

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Reprinted from Ecology, Vol. 45, No. 2, Spring 1964

RELATIONSHIP OF WEATHER TO MIGRATORY MOVEMENTS OF BLACK-TAILED DEER

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Abstract. A study of the influence of weather factors on the migrations of a herd of black-tailed deer showed that periods of migration as indicated by night spotlight samples were closely correlated with seasonal changes in minimal relative humidity. Both spring and fall migrations, and possibly an atypical summer movement, occurred during ranges of 40 to 60% minimal relative humidity. Snowstorms, rainfall, absolute humidity, and temperature were not so closely correlated. The migrations could not be attributed to habitat factors such as food, water, or escape cover.

INTRODUCTION

Many herds of deer in the western United States migrate from high mountainous summer ranges to protected valleys for the winter, only to return again with the warm weather of spring. Downward migrations in the fall are frequently spectacular; thousands of deer may move over long distances in a matter of several days. These migrations are usually associated with severe fall snow storms (Leopold *et al.* 1951; Russell 1932; and many others). Yet a number of instances of fall migrations occurring substantially before fall storms have been reported (Russell 1932; Fischer *et al.* 1944; Rasmussen 1941). In these herds the fall migration takes the form of a gradual, almost imperceptible drift of deer from the high elevations. It occurs with gradual seasonal changes in weather so that relationships with environmental factors are difficult to determine. This type of migration is probably more common than is generally supposed, but has been overlooked because of its subtle nature.

Migrations in the spring usually progress as a slow upward movement of individuals or small groups, and are influenced by factors that are largely unknown. It has been shown by Leopold *et al.* (1951) and this research that spring migrations are not controlled by snow distribution. Russell (1932) and Leopold *et al.* have suggested that the upward movement may be controlled by development of new green growth, but this idea is not well substantiated and is contradicted here. Darling (1937) found that insect harassment was important in some upward movements of red deer in Scotland, but this, too, was not important in the present study.

In 1958 a study of the migratory patterns of a herd of black-tailed deer (*Odocoileus hemionus columbianus*) having an early and gradual fall migration preceding storm conditions was made in the west-central Cascade Mountains of Oregon.[2] This paper attempts to correlate the movements of this herd with seasonal changes in weather factors. Ultimately this migration removes the deer from an area unsuitable for winter occupancy because of snow. But the reasons why it takes place so far in advance of the occurrence of snows are not understood.

The study was conducted in the H. J. Andrews Experimental Forest, a 15,000-acre tract in the Willamette National Forest near Blue River, Oregon. The experimental forest is bordered by 3 main ridges which form a rough triangle and encompass the Lookout Creek drainage. The triangle is open at its western point where Lookout Creek joins Blue River. Elevations range

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[2] Oregon Agricultural Experiment Station Technical Paper No. 1445.

from approximately 1,500 ft at this confluence to a maximum of 5,300 ft. Climate is typical of the north Pacific coast region where winters are high in precipitation and summers are relatively dry and warm. In the Andrews Forest area winter snow lines typically fluctuate about the 1,500 elevation level.

Most of the area is covered by virgin old-growth timber which forms a dense canopy high above the forest floor. Douglas fir (*Pseudotsuga menziesii*) is the predominant species, but commonly interspersed with it are western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). Vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and rhododendron (*Rhododendron macrophyllum*) are characteristic of the sparse understory.

Since logging began on the Andrews Forest in 1950, approximately 1,200 acres of timber have been clear-cut from staggered units or blocks. Cleared units range in size from less than one to approximately 70 acres and average about 33 acres. The units were control-burned to reduce the fire hazard of slash remaining from the logging operation. Herbs and shrubs form a dense luxuriant growth in the exposed areas and furnish excellent summer range for deer, which occupy the area from about April through September. Common species utilized as food by deer include fireweed (*Epilobium angustifolium*), vine maple (*Acer circinatum*), trailing blackberry (*Rubus vitifolius*), thimbleberry (*Rubus parviflorus*), big-leafed maple (*Acer macrophyllum*), elderberry (*Sambucus* sp.), and willow (*Salix* sp.).

The Andrews Forest herd winters in the lowlands and on exposed south slopes in the MacKenzie drainage south of the Andrews Forest. This winter range is shared with deer from other drainages in the river system, as well as with a small population resident in the area throughout the year. The upper limit is set by the snow line, and as little as 3 or 4 in. of new snowfall will drive deer to a lower level. The plant cover is much the same as that of Andrews Forest, but of a somewhat poorer quality for deer range since the land generally was cleared much earlier and hence is in a later successional stage. The difference is in quality rather than quantity.

Fawning occurs in June and early July while the herd is on the Andrews Forest summer range. The rut occurs on the wintering grounds in November and December, long after the fall migration of the Andrews herd. Since this is a time of intermingling of several local herds, the Andrews Forest deer do not constitute a well-defined genetic population.

Methods

To obtain a continuous record of the numbers of deer within the study area, twice-weekly night spotlight samples were taken from the time of the spring migration in April until the end of the fall migration in September. The technique involved driving the road system of Andrews Forest at night, while sweeping the area on each side of the road with a powerful spotlight beam. Deer in the vicinity were easily sighted when their eyes reflected the light back to the observer. The method was extremely effective in the logged areas, where deer were frequently sighted in the heaviest vegetation. There was no evidence that deer failed to look toward the spotlight as the vehicle moved through the units. If it stopped, deer accustomed to the light would sometimes ignore any amount of whistling, shouting, horn-blowing, or spotlight flashing. But without fail, moving the vehicle would again bring their attention. It was not necessary for the deer to look directly at the light since their eyes reflect through a considerable angle. Bedded deer, if anything, were more easily sighted than active deer since open areas with a good view were preferred for night-bedding sites, and these deer watched the light far more steadily than those actively feeding. Thirty to 50% of the deer spotlighted were bedded, and no relationship was apparent between the per cent of deer bedded and the size of the count.

Sampling was begun one to 2 hr after darkness, and was completed in 3 to 4 hr depending upon the number of deer sighted. Because of the small unit size and absence of obstructions, spotlight coverage of the logged units was almost complete. Attempts to spotlight in virgin timber were ineffective because of the complete barrier of the trunks in a short distance. The number of deer observed was used as an index of the population present.

Weather data used in the analysis were obtained from a weather station maintained in the Andrews Forest by the U. S. Forest Service. The station was situated in the edge of the timber approximately 1,600 ft from the bottom of the drainage. Weather factors, of course, vary, depending upon exposure, elevation, vegetation type, and many other variables, and the readings obtained from this one station are not representative of the Andrews Forest as a whole. The deer can move from one climatic regime to another merely by walking from the logged areas into the timber, and no one set of readings can possibly reflect the weather conditions immediately surrounding the animals.

Yet several circumstances reduce these difficulties considerably. Relative humidities at night invariably approached saturation, so that conditions were relatively uniform throughout the area, particularly for vegetative-type and slope exposure. It seems reasonable to expect that temperature gradations with change in altitude were also greatly mediated by these conditions. Thus the night spotlight samples were taken during times when the most uniform weather conditions prevailed throughout the area.

Also, during times of extreme high daytime temperatures and low relative humidities—the 2 weather factors receiving greatest stress in this paper—the deer were restricted to the timbered areas. Therefore it is probable that readings obtained from the station in the timber were closer to the actual weather surrounding the deer than would be the unquestionably more severe conditions extant in open logged areas.

Although these favorable circumstances by no means circumvent the problem, it seems the readings obtained give a generally valid reflection of the changes in weather which occurred, and perhaps even a reasonable estimate of conditions actually impinging upon the deer.

Results

Migrations

Spring migration.—The first sign of the spring migration was observed in mid-March when upward movements of deer from the winter range became apparent. In April, deer began to drift into the Andrews Forest. Spotlight samples

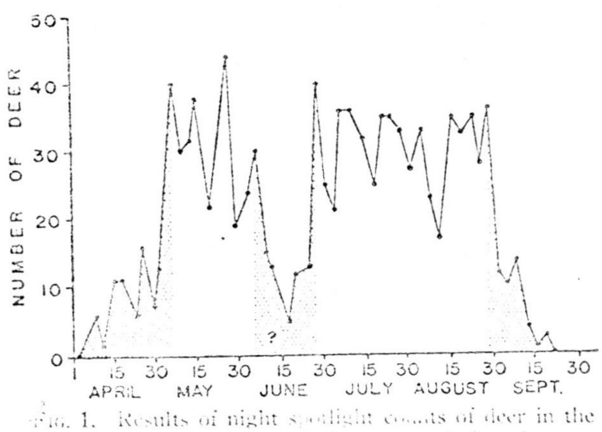

Fig. 1. Results of night spotlight counts of deer in the Andrews Forest used as an index to population changes. Shaded areas represent periods of movement of deer to or from the area. The balance of evidence indicates that the June decline was a "reverse migration" but this was not positively established.

were begun April 2, and the first deer were sighted April 8. Results of the spotlight samples of the area are shown in Figure 1. On the last days of April and during early May, the number of deer returning to summer range increased rapidly, and the bulk of the herd had returned to the Andrews Forest by mid-May as evidenced by a general leveling off of the numbers of deer sighted. Movement of deer into the area was not controlled by distribution of snow. Although some snowdrifts remained at higher elevations, the forest was mainly clear of snow several months before the migration.

Fall migration.—The fall migration of the Andrews Forest population began early in September, and by September 20 the herd was essentially absent (Fig. 1). After that date no further direct observations of deer were made, although fresh tracks were occasionally found in the area. The fall migration occurred long before inclement weather began. The first snow fell November 13, nearly 2 months after deer had left the experimental forest. The timing of this snowfall is more or less typical for the area. Although light skiffs of snow frequently occur earlier, particularly at higher elevations, a heavy snow fall would be quite unusual before late October.

The Andrews Forest summer range is in close proximity to the winter grounds, so distances covered by migrations were short. A part of the herd crossed over the south ridge of the drainage, a trek of approximately 2 miles. The remainder of the herd moved along the drainage, a distance of about 6 to 8 miles from the summer to the winter range.

The only other major fluctuation in the spotlight sample results occurred during June (Fig. 1). The full summer population, which had arrived in May, fell to as low as 5 deer by June 17. However, the population had again increased by June 27 when a count of 40 deer was obtained.

That this June decrease represents a real change in numbers not related to normal fluctuations inherent in sampling can be tested statistically. If the samples taken from May 6 through June 7 and from June 27 through August 29 are combined, a total of 28 samples of the normal summer population is obtained exclusive of movements to and from the study area. Attempted correlations of these samples with temperature and humidity failed to show any relationship. Thus the resulting variation in these spotlight counts must be considered to be the normal variation of the method due to undetermined factors. When the 5 low points in June were tested as a group to see if they belonged to the above-defined group they were found to be very different statistically ($t = 5.75$ with 31 df). However, considering the 5 June points as a normal population is, perhaps, unsound since they indicate a falling population followed by a recovery, without a single point deviating from the pattern. Still, the June points can be tested statistically against the larger group as single observations, according to the method given by Simpson, Roe, and Lewontin (1960). The June observations of 15, 13, and 12 are significantly different at the 2.5% level ($t = 2.14$, 2.42, and 2.56, each with 27 df), and the observation of 5 deer is significantly different at the 0.5% level ($t = 3.538$ with 27 df). In view of these statistics and the consistent pattern of the observations there seems to be little doubt that the June decline represents a change related to the deer rather than to the sampling technique.

WEATHER

Rainfall.—The pattern of rainfall during the study period is shown in Figure 2. The normally heavy rainfall of the winter months continued through June. However, in July and August almost no rainfall occurred. Heavy fall rains began in September, and except relatively low amounts in late September and early October, high precipitations were maintained into the winter.

FIG. 2. Precipitation in the Andrews Forest by 2-week periods from April to mid-November, 1958. High precipitation continues throughout the winter months.

Temperature.—When temperature records for the periods of deer occupation were examined it was found that the minimal daily temperature (the extreme low during the night) varied only slightly. The total range was only slightly more than 10°, and usually the low fluctuated about the mid-point. No directional change during the migratory period was apparent in the minimal temperatures. However, maximal daily temperatures did show considerable variation during the study. Because of the essentially constant nature of minimal daily temperatures it seemed advisable to use maximal temperatures rather than mean daily temperatures in attempted correlations with deer activities. To use the mean temperatures would, in effect, reduce the temperature "sensitivity" by one-half; also, the extreme seemed to be more significant in the migratory responses of deer.

Relative humidity.—The pattern of relative humidity was similar to that of temperature. Maximal relative humidity which occurred during the night was essentially a constant. Only on 5 nights was it less than 90% and only once below 85%. That maximal humidity as well as minimal temperature was essentially a constant is not surprising in view of the relationship between the 2 factors. Minimal relative humidity showed great variation, and this entity was used in preference to mean relative humidity for the same reasons given for the choice of maximal temperature rather than mean temperature.

Relationship between temperature and humidity.—The relationship between maximal daily temperature and minimal daily humidity in the Andrews Forest during the study period is shown in the climograph which forms the base plane of Figure 3. For convenience hereafter, the terms "temperature" and "relative humidity" or "humidity" will be used as synonyms for maximal daily temperature and minimal daily relative humidity, respectively. The climograph of Figure 3 was constructed by plotting the mean temperature for a 2-week period against the mean relative humidity for the same 2 weeks. Points representing the first 2 weeks of a month are designated by

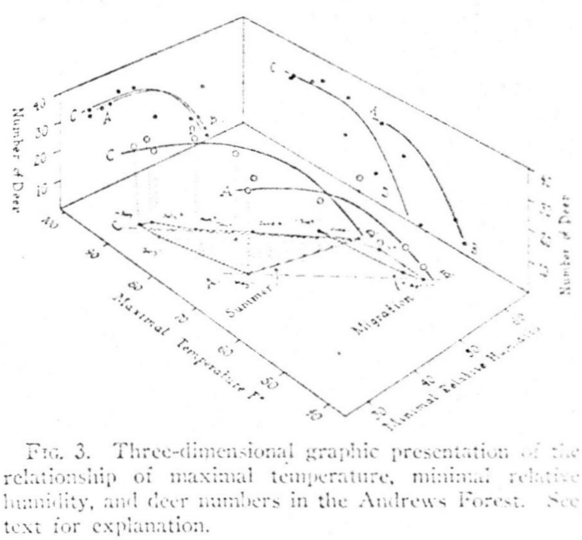

FIG. 3. Three-dimensional graphic presentation of the relationship of maximal temperature, minimal relative humidity, and deer numbers in the Andrews Forest. See text for explanation.

a minus sign and those of the second 2 weeks by a plus sign.

In general, the relationship between temperature and relative humidity showed 2 separate seasonal regressions indicated by lines (located by eye) in Figure 3 which are designated A-B and C-D. These regressions are substantiated by data for the remainder of the year, omitted from the figure since deer do not occupy the forest during that period. The lower regression represented by the spring months is separated by approximately 20°F from the upper regression which includes the summer and fall points. Examination of weather data for 1959 showed a similar pattern, and this is probably typical for the Andrews Forest.

The areas of the climograph covering times when deer were on the summer range and in the process of migration are indicated. During the migratory periods the means of temperature ranged from 52 to 72°F, while means of relative humidity ranged from only 52 to 57%.

Note that a pronounced irregularity from the generalized pattern occurred during June when unusually high relative humidities occurred. Observe that the climograph point in Figure 3 for the first 2 weeks in June fell in a range of weather typical for periods of deer migration.

In Figure 3 the numbers of deer sighted by the spotlight method are plotted as a 3d dimension over the temperature-humidity climograph. The 3d dimension points are based upon the mean number of deer obtained by the spotlight counts for the same 2-week periods. For example, the first 2 weeks of May had a mean of maximal daily temperatures equal to 71.1 and a mean of minimal daily humidities of 37.0. Four spotlight samples were taken during this 2-week period, and the mean number of deer sighted per sample was 28.8. This value is represented by a point in the 3d dimension above the weather data point in the climograph. Thus, since spotlight samples were taken twice weekly, each point in the 3d dimension is based upon the mean number of deer sighted in 4 night samples during that particular 2-week period. An exception is July when 5 samples were taken in each 2-week period.

It can be seen that the 3d dimension points in Figure 3 form 2 separate arrays of points, each one overlying a regression of humidity on temperature on the climograph base. Curves, located by eye, are drawn through the 2 arrays of points and labeled (A-B and C-D) in the same manner as the temperature-humidity regressions with which they are associated.

The 3d dimension curves and the points upon which they are based are shown in the upper left plane of Figure 3 as they would appear if projected from the relative humidity axis. The upper right plane shows the same curves and points as projected from the temperature axis. In essence, the plane on the upper left shows a simple plotting of deer on humidity, and the upper right plane shows deer on temperature.

The reader might rightly wonder if the presentation in Figure 3 is not unduly complicated. However, simple plotting of deer against humidity and deer against temperature, followed by a comparison of the results, could lead to difficulties. There would probably be a tendency to attempt a single curve in each graph to best fit the points followed by a comparison of the nearness of fit of the curves. This would overlook the temperature-humidity relationships which indicate 2 separate curves as demonstrated in Figure 3 and obscure the nature of the relationships between the 2 weather factors and their seasonal changes, and the number of deer observed.

Discussion

Habitat

Unsuitable environment was not believed responsible for the fall migration. An abundance of browse of preferred species, water, and escape cover remained on the summer range, and, although detailed measurements were not taken, no obvious change in these factors was apparent at the time of the migration. Changes in nutritional properties of browse were probably not involved. Dealy (1959) showed that crude protein values of favored browse species do not undergo significant changes at this time. Also, the nearness of the winter range, which supports the same plant species, would lead one to expect similar changes in both areas.

Difficulties are also encountered in attributing the spring migration to environmental changes. Here again water and escape cover in the form of standing timber were in superabundance. And emergence of the new spring growth was started well in advance of the migration.

Photoperiod

Correlations with constant seasonal phenomena such as photoperiod change were not attempted, since the timing of the migration periods was known to vary as much as 2 to 3 weeks from year to year. This, of course, does not rule out the existence of photoperiod influences. However, if such a primary stimulus does exist, it is subject to substantial modification by local environmental conditions, which are worthy of study in their own right.

RAINFALL

If the deer numbers in Figure 1 are compared to the precipitation record for the Andrews Forest in Figure 2 it can be seen that there is a general relationship between the 2. Yet detailed comparison demonstrates a number of discrepancies. For example, the spring migration was well underway during late April when nearly 7 in. of rain fell. The fall migration continued in the second 2 weeks of September even though less than an inch of precipitation occurred during this period and a similar amount in the first 2 weeks of October. A total of only 2.69 in. of rain fell during the fall migration period as compared to 9.06 in. during the spring migration.

In spite of these inconsistencies a general correlation does seem to be present. Direct effects of rainfall upon deer activities were not apparent. Deer were routinely observed feeding during rainfall and seemed oblivious to the wetness, although a higher percentage of the animals were bedded, as opposed to active, in the spotlight samples taken during periods of falling rain. However, some of the highest counts were made during rainfall.

In view of these data it was felt that the direct effects of rain upon deer migrations were probably slight, and its primary importance lay in its influence upon both temperature and relative humidity.

TEMPERATURE AND RELATIVE HUMIDITY

These two weather factors are discussed in the same section because of the difficulty in separating their influences upon animals.

It is apparent that the 3d dimension curves in Figure 3 are essentially the same when projected from the relative humidity axis as evidenced by their overlapping as seen in the upper left plane. Thus it appears that the correlation of numbers of deer with minimal relative humidity was the same for both migrations in spite of a difference of about 20°F in maximal temperature between the spring and fall migrations. These results suggest that migrations of this herd were closely related to relative humidity.

Conversely, projection along the temperature axis gives a divergence of the curves and consequent poor fit of the points. The very broad correlation of deer numbers with maximal temperature was probably owing to its association with humidity rather than with deer responses. Similar analysis of absolute humidity also gave a poor correlation with deer numbers.

The spring migration began when minimal relative humidity dropped below approximately 60% and was completed by the time it reached about 40% (Fig. 3). The leveling off of the curves at 30 deer is assumed to indicate the arrival of the full summer deer population. The fall migration began when minimal relative humidity increased above 40% and was completed by the time it reached 60%. These responses may indicate the existence of "thresholds" which trigger the movements of the herd. However, it should be noted that movements of the deer were not immediate, but rather, were related to the cumulative minimal relative humidity during a period of 5 to 7 days. This flexibility of behavior would seem to prevent triggering of frequent large-scale deer movements by a factor that can fluctuate widely for a short period of time as relative humidity does.

The fact that high minimal humidities, typical of humidities during migrations, occurred during the first 10 days of June and were followed shortly by a marked drop in spotlight counts may be significant. The population returned to normal level by July, again correlated with the resumption of a normal range in minimal relative humidity. This decline in the numbers of deer in the logged area may have been due to the occurrence of a "reverse migration." However, insufficient information of the actual whereabouts of the herd was obtained to establish conclusively that the decline was a movement from the Andrews Forest rather than an exceptional restriction of deer to the timbered areas. In view of observations of deer activities during high minimal humidities at other times, the latter explanation seems implausible. For example, counts as high as 40 deer were obtained during the summer in periods of actual rainfall when relative humidity was 100%. And recall that night humidities when the spotlight counts were taken were normally near 100%. These considerations reemphasize that the migrational responses reported here are in relation to continued periods of high relative humidity. It might be argued that restriction of deer to timbered areas is a response to this continued high relative humidity and accounts for the June decline in numbers. But spotlight samples taken on the winter range during December when relative humidity was continually at or near 100% gave no evidence of such a restriction. Deer were found to be feeding or resting in the cleared areas in a normal manner. Of course the response of deer to a given relative humidity may vary at different times of the year.

It would be reasonable to expect that if the deer were restricted to timbered areas at night, higher daytime feeding in the logged areas would occur, permitted by the moderate daytime weather conditions prevailing at this time. During June and July, daytime samples were taken in the mornings on the same days as the night spotlight samples, and by watching for deer while driving the road system of the area in the same manner as for the night samples. Although numbers of deer recorded were much lower in the daytime sample than in the night samples, they followed the same over-all pattern. Five samples during the decline averaged 3.4 deer per sample (range 1 to 5) whereas 12 samples taken before and after the decline averaged 6.3 deer per sample (range 0 to 18). The difference between these means is not statistically significant ($t = 1.324$ with 15 df) but the results argue against an increase in daytime feeding and lend weight to the "reverse migration" hypothesis.

A further complication of the June decline is that it coincided more or less with the beginning of fawning, and at the time this was thought to be responsible for the drop in spotlight counts. Several days of intensive searching for fawns failed to turn up any evidence, although this is not surprising in view of the extremely heavy cover available. However, the most serious flaw in this interpretation is the fact that the spotlight counts returned to normal in the last few days of June (40 deer on June 27) though fawning continued at a fairly high level through early July. The behavior of the doe in hiding the newborn fawn while she ventures out to feed is too well known to repeat here. Lactating females feeding in the logged units without accompanying young was the rule throughout July spotlight samples. Unfortunately it was impossible to establish whether the does observed in the logged units immediately following the recovery of deer numbers had fawned early or late, and the relationship of decline and recovery of the sample deer counts and fawning activity are necessarily based on population values. However, one doe actively feeding in a logged unit on the night of July 8 was positively established as the mother of a recently born fawn still shaky on his legs and easily captured by hand. The difficulty of does with new fawns performing movements must also be considered, and would account for perhaps a 4- to 5-day delay of the does dropping fawns during the decline and recovery periods. The influence of this factor would be of an order of magnitude well below the sensitivity of the sampling technique used.

The balance of evidence seems to favor the "reverse migration" interpretation, but in view of the lack of a positive demonstration and of the variables involved, the question is perhaps best left open.

Although the migrations were closely correlated with minimal relative humidity, it cannot be determined from present data if humidity exerts a direct causal effect. The deer may be influenced by some other environmental factor (e.g., food) which may also be correlated with humidity, or it may serve as a modifier of a primary stimulus such as photoperiod length. An indication of a direct humidity effect would be given by the drop in deer numbers correlated with the unseasonally high minimal humidities during June if the decline could be adequately established as due to a movement from the summer range by the herd.

It should be reemphasized that the primary purpose of using these extremes rather than means is a matter of convenience in establishing correlations between these factors and deer movements by using the most sensitive measure available. This procedure should not be interpreted as meaning that the responses of deer can be attributed definitely to the extremes per se; however, the results seem to suggest that the extremes are more significant.

The responses of deer measured in this study are not comparable to the behavioral changes in response to weather conditions reported for red deer in Scotland by Darling (1937). He found that movements and "irritability" were associated with immediate weather changes, particularly those involving humidity. Immediate effects were not detected in the present study. Familiar groups were consistently sighted in successive spotlight samples in the same places regardless of current weather conditions, and no change in tendency to flee was observed. However, deer spotlighted at night from a vehicle are remarkably lacking in excitability, and more complete daytime observations might demonstrate responses in these animals similar to those of red deer.

That deer are sensitive to relative humidity has been noted by previous workers. Linsdale and Tomich (1953), working on the Hastings Reservation in Monterey County, California, found that relative humidity was an effective regulator of deer activity, and Hahn (1949) reported that the activities of white-tailed deer on the Edwards Plateau of Texas were markedly influenced by relative humidity. However, no reference to the apparent relationship between humidity and migration as indicated by this study has been found.

ACKNOWLEDGEMENTS

I wish to thank Arthur S. Einarsen and William Lightfoot for advice in conducting the field work; Daniel

W. Coble aided in taking night spotlight samples. Weather data were obtained through the courtesy of the U. S. Forest Service. Charles E. Warren, A. Starker Leopold, and Peter A. Jordan read and suggested substantial improvements of the manuscript. Gene M. Christman drew Figure 3.

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