6. Summary

Sexing Reed Warblers (*Acrocephalus scirpaceus*) by the cloacal region and the brood patch.

The development of the cloacal region and the prood patch between may and september is described and its relation to the proceeding of breeding time is shown.

Reed Warblers can be sexed by examining the cloacal region and the brood patch during the time of breeding and in some cases also during migration. ♀ show no bulbous of the cloaca, none of the caught ♂ possessed a brood patch. It is proved that there are unpaired ♂ and obviously ♀ in breeding populations of Reed Warblers.

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The Moon: a Neglected Factor in Studies on Collisions of Nocturnal Migrant Birds with Tall Lighted Structures and with Aircraft

By F. J. Verheijen

1. Introduction

Man has created a variety of hazards for nocturnal migrants. Bird kills have been reported at high lighted structures, such as lighthouses, tall buildings, ceilometers, radio and television towers. In the course of several nights over 1000 migrants have been killed at one television tower. On three successive nigths in the autumn of 1954 mass kills were reported, and on the night of October 7—8 75,000 birds were reported killed at four ceilometers in Alabama and Georgia (Terres 1956). In 1966 it was estimated that TV towers in the USA took an annual toll of more than a million birds (Aldrich et al. 1966). Several authors have expressed concern about this bird mortality. They have tried to describe the birds' behaviour around the lights, and have suggested explanations for the phenomenon. They have stressed that every effort should be made to encourage research in this area in order to obtain a fuller understanding of the phenomenon. Only then will there be a basis for developing ways of preventing, or a least reducing mortality. Nevertheless it was admitted recently (Avery et al. 1976) that „the primary question of what features of lights cause birds to congregate at tall lighted structures under overcast conditions is still unanswered".

Lighthouses were the first major man-made trap for nocturnal migrants. In an extensive work (Clarke 1912) the weather conditions correlated with mass bird kills at lighthouses were characterized by rain, haze, clouds, drak starless nights. The illumination of a lighthouse and its immediate environment seems to protect birds to some extent (VERWEY 1924—28). However, the effectiveness of floodlighting seems to be variable (AVERY et al. 1976). Between 1946 and 1956 the highest bird mortality was reported at stationary ceilometers at airports. Since then these cloud height sensors have been equipped with a rotating light beam so that they became much less of a problem to migrants. In the meantime radio and television towers supplied with warning lights for aircraft have become an increasing hazard to migrants (ALDRICH et al. 1976). The bird/aircraft collision problem, which has not been solved either (review: LARKIN 1976), demonstrates that man may be a victim as well as the birds.

Recently I came across data about twelve instances of bird mortality at airport ceilometers in the USA reported by a number of authors between 1948 and 1952 and summarized in tabular form by HOWELL et al. (1954). The table includes data about the prevailing atmospheric conditions: cloud type, ceiling height, wind direction and speed, visibility, and occurrend of fog or rain. Presumably these conditions affected both the number of migrants in the air and the degree to which they congregated at, and were killed at a given ceilometer.

I was struck by the absence in this table of any data about the moon because there is overwhelming evidence that insects, fishes and birds generally congregate at artificial lights on nights during which the moon is nearly new, or during the part of the night when the moon is below the horizon (VERHEIJEN 1958, 1960, 1969; BEN YAMI 1976).

I have the impression that among ornithologists, at least in the USA, the moon has been regarded as irrelevant because it is invisible in the weather conditions which are conducive to kills. Obviously it is true that in these weather conditions the moon is invisible as a point source. Anyone who has been out in the field and far away from man-made illuminations knows, however, that our capacity for recognizing the environment and for identifying objects by sight on overcast nights varies greatly according to whether there is a full moon or a new moon. For details about the irradiance of the night sky (zodiacal light, star light, moonlight) see MUNZ & MCFARLAND (1977). Obviously the atmospheric condition and the moon-age should be considered as independent variables with respect to their influence on vision at night. Since it is generally assumed that the lunar cycle does not influence atmospheric conditions — the improbability of the reverse causal relation is self-evident — the occurrence of bird kills at night might be correlated with the lunar cycle as well as with atmospheric conditions.

Therefore it seemed worthwhile to determine whether the nights on which bird mortalities at tall lighted structures have been reported show some correlation with the lunar cycle. Because the nocturnal collision of birds with aircraft — whether or not the latter were equipped with landing or warning lights — seemed to me to be another instance of the failure of visual or photic orientation, I also searched through the relevant literature for data about the moon.

2. Bird Kills at Tall Lighted Structures

I found 62 nights with reported bird kills in the USA between 1935 and 1973. Although there are likely to have been many more such nights, there is no reason to suppose that these 62 nights are not fairly representative. Fifty-seven of these nights occurred during autumn migration, and the remaining 5 nights during spring migration. As far as I could verify, the moon was referred to in only three publications. With respect to the Washington Monument is was stated by OVERING (1936) that „Nearly all birds struck the monument when there was no moon“. When the „sky was clear . . . and the moon almost full“ HOWELL et al. (1954) „saw only two possible birds pass high and rapidly through the beam“ of the ceilometers at Knoxville, Tennessee, on the night of October 1—2, 1952. From records of bird casualities at a Florida TV tower during the period 1955—1961 STODDARD (1962) concluded: „So far we cannot see that the phase of the moon has much bearing on the number of birds migrating, or striking the obstruction. However, additional figures over the years may show differently“. The weather bird-kill relationship was characterized by this author as follows: „A rare combination of deep, low clouds with mist and murk and favoring winds, sets the stage for disaster“. In numerous other publications, including a recent one (AVERY et al. 1976) with the „most complete description yet of the behavior of nocturnal migrants at a tall tower“, no mention is made of the moon in the environmental data.

Table 1: Moon-age on 62 nights with bird mortalities. The synodic lunar month is assigned 30 lunar days.

	Date		Moon-age	Locality; big kills specified	Reference
1935	Sept.	6— 7	8	Washington Monument	Overing 1936
1936	Sept.	17—18	1	Washington Monument	Overing 1936
	Sept.	18—19	2	Washington Monument	Overing 1937
1937	Sept.	12—13	7	Washington Monument	Overing 1937
	Sept.	26—27	21	Washington Monument	Overing 1938a, b
1948	Sept.	9—10	5	Ceilom. Nashville, Tenn.	Spofford 1949
	Sept.	10—11	6	TV tower, Baltimore	Spofford 1949
1950	April	25—26	8	Ceilom. Selma, Ala.	Parrish (in Howell et al. 1954)
	Sept.	19—20	7	Ceilom. Mitchell A. F. Base, Long I. and McGuire A. F. Base, N. Y.	Arbib (in Howell et al. 1954)
1951	May	6— 7	30	Floodlight recreation area Gulf Coast, Texas (> 10,000)	James 1956
	Oct.	7— 8	1	Ceilom. Knoxville, Tenn. (> 1000) Ceilom. Smyrna, Tenn. (± 1000)	Howell & Tanner 1951 Laband 1951
1952	May	23—24	0	Madison, Wisc.	Hickey (in Howell et al. 1954)
1954	Oct.	5— 6	8	Several ceilom. and TV towers (> 10,000)	Howell 1955 Johnston 1955 Johnston & Haimes 1957 Terres 1956
	Oct.	6— 7	9	Several ceilom. and TV towers (> 10,000)	
	Oct.	7— 8	10	Several ceilom. and TV towers (± 75,000)	
1955	Sept.	23—24	8	TV tower Champaign County, Ill.	Brewer & Ellis 1957
	Sept.	24—25	9	Ceilom. Nashville and Smyrna, Tenn.	Laskey 1956
	Oct.	6— 7	20	TV tower Champaign County, Ill.	Brewer & Ellis 1957
	Oct.	8— 9	22	TV tower Leon County, Florida (± 2000)	Stoddard 1962
1957	May	29—30	0	TV tower Champaign County, Ill.	Cochran & Graber 1958
	Sept.	19—20	25	TV tower Eau Claire, Wis. (> 20,000)	Kemper 1958
	Sept.	21—22	27	TV tower Champaign County, Ill.	Graber 1968
	Oct.	4— 5	10	TV tower Leon County, Florida (2315)	Stoddard 1962
	Nov.	4— 5	12	TV tower Champaign County, Ill.	Cochran & Graber 1958
1958	Sept.	15—16	2	TV tower Champaign County, Ill.	Graber 1968
	Sept.	16—17	3	TV tower Champaign County, Ill	Graber 1968
1959	Sept.	28—29	25	TV tower Champaign County, Ill.	Graber 1968
1960	Sept.	19—20	29	TV tower Champaign County, Ill.	Graber 1968
1961	Sept.	3— 4	23	TV tower Eau Claire, Wis.	Raveling 1965
	Sept.	11—12	1	TV tower Eau Claire, Wis.	Raveling 1965
	Sept.	13—14	3	TV tower Eau Claire, Wis.	Raveling 1965
1962	Sept.	9—10	10	TV tower Eau Claire, Wis.	Raveling 1965
	Sept.	10—11	11	TV tower Eau Claire, Wis.	Raveling 1965
	Sept.	24—25	25	TV tower Champaign County, Ill.	Graber 1968
	Oct.	2— 3	4	TV tower Eau Claire, Wis.	Raveling 1965
1963	Sept.	18—19	0	TV tower Eau Claire, Wis. (± 30,000)	Kemper 1964
	Sept.	19—20	1	TV tower Eau Claire, Wis.	Kemper 1964
	Sept.	10—21	2	TV tower Eau Claire, Wis.	Kemper 1964
1969	Sept.	10—11	28	TV tower near Bithlo, Orange Co, Florida	Taylor & Anderson 1973
	Sept.	13—14	1	TV tower near Bithlo, Orange Co, Florida	Taylor & Anderson 1973
	Sept.	29—30	18	TV tower near Bithlo, Orange Co, Florida	Taylor & Anderson 1973
	Oct.	4— 5	22	TV tower near Bithlo, Orange Co, Florida	Taylor & Anderson 1973
	Oct.	17—18	6	TV tower near Bithlo, Orange Co, Florida	Taylor & Anderson 1973

Date			Moon-age	Locality; big kills specified	Reference
1970	Sept.	28—29	27	TV tower near Bithlo, Orange Co, Florida (1592)	TAYLOR & ANDERSON 1973
	Sept.	29—30	28	TV tower near Bithlo, Orange Co, Florida (859)	TAYLOR & ANDERSON 1973
	Oct.	17—18	17	TV tower near Bithlo, Orange Co, Florida	TAYLOR & ANDERSON 1973
1971	Sept.	24—25	5	TV tower near Bithlo, Orange Co, Florida	TAYLOR & ANDERSON 1973
	Oct.	7— 8	18	TV tower near Bithlo, Orange Co, Florida	TAYLOR & ANDERSON 1973
	Oct.	10—11	21	TV tower near Bithlo, Orange Co, Florida	TAYLOR & ANDERSON 1973
	Oct.	11—12	22	TV tower near Bithlo, Orange Co, Florida	TAYLOR & ANDERSON 1973
	Oct.	17—18	28	TV tower near Bithlo, Orange Co, Florida	TAYLOR & ANDERSON 1973
	Oct.	19—20	30	TV tower near Bithlo, Orange Co, Florida	TAYLOR & ANDERSON 1973
1972	May	10—11	26	Omega TV tower, North Dakota	AVERY et al. 1977
	May	14—15	1	Omega TV tower, North Dakota	AVERY et al. 1977
	Aug.	21—22	12	Omega TV tower, North Dakota	AVERY et al. 1977
	Sept.	1— 2	23	TV towers in central Illinois	SWEETS & BOHLEN 1977
	Sept.	26—27	19	TV towers in central Illinois (± 2800)	SWEETS & BOHLEN 1977
	Sept.	28—29	21	TV towers in central Illinois	SWEETS & BOHLEN 1977
	Oct.	4— 5	27	Omega TV tower, North Dakota	AVERY et al. 1977
	Oct.	30—31	22	TV towers in central Illinois	SWEETS & BOHLEN 1977
1973	Sept.	25—26	28	Omega TV tower, North Dakota	AVERY et al. 1977
	Oct.	4— 5	7	Omega TV tower, North Dakota	AVERY et al. 1977

The moon-ages on the 62 reported nights were ascertained (Table 1), and considered to be a sample of a circular distribution of nights in a lunar month. With respect to the application of circular statistics to this distribution of nights some aspects deserve closer attention. First, it could be suggested that the activities of the observers were correlated with the lunar cycle. It seems justified to assume that this was very unlikely since almost all observers were preoccupied with the weather as the fatal factor. Moreover some authors visited the relevant locality at daybreak every day and for prolonged periods, sometimes even for years, spotting bird casualities with painstaking care. Secondly it must be decided whether the circular sample — the respective nights with kills — is to be regarded as consisting of vectors of the same length or of different length. It seems self-evident that a night on which ten thousand bird kills were recorded should be given more weight than a night with only ten kills. However, the uncertainty as to the actual number of victims on a given night and at a given locality has been stressed by more than one author. STODDARD (1962), for instance, analysed in detail why the records represent only a minimum estimate of the total number of birds that fall to the ground. There is no sharp distinction between birds that are dead, almost dead, severely injured, only slightly crippled, stunned or perhaps only exhausted. The last few categories of birds may try, and manage, to fly away as the observer approaches. Moreover Stoddard amphasized as did others, that a considerable proportion of the fallen birds is often removed incredibly quickly, at least in the deep South East of the USA, by a variety of predators: mammals, birds, and invertebrates. Besides, the type of area involved — open ground, grass and weeds, crops, shrubs, wood — hampers any kind of quantifiable inspection.

Another obstacle in estimating the gravity of a given kill, for instance in terms of the affected percentage of migrants locally in the air at a given night, is that both the prevailing atmospheric conditions and the lunar cycle affect the nocturnal migration activity in a complicated way that is not yet fully understood (see discussion).

The majority of published reports mention kills of a dozen or two per night and the locality. Kills from ten up to several hundreds of birds are mentioned or listed separately by most authors. Huge kills exceeding of 1,000, and even up to 10,000 birds on a given night have sometimes been recorded at more than one locality and by more than one author. Such nights have become notorious as „big nights“. Most of the nights (48) listed in Table 1 are of the „ten up to several hundreds“ type, and a smaller number (14) are „big nights“.

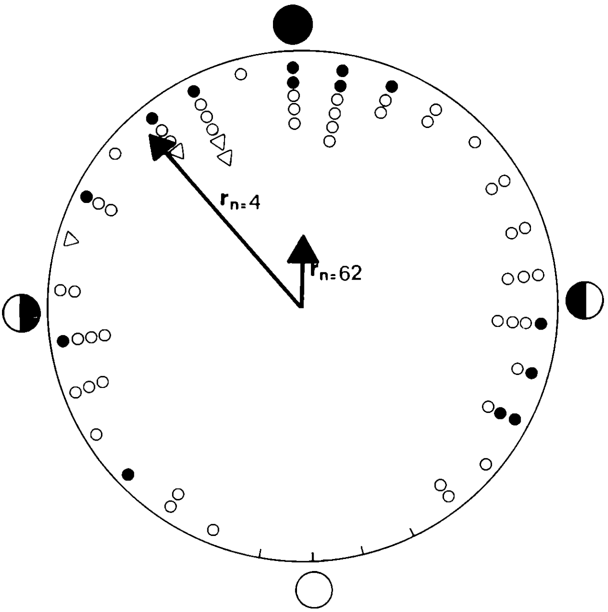

Fig. 1: Frequency distribution in a lunar month of the nights on which birds were reported killed (62 nights) or congregated (4 nights). The synodic lunar month is assigned 30 lunar days. ●, ◐, ○ and ◑ indicate new moon, first quarter, full moon and last quarter respectively; o night with moderate kills; • night with big kills; △ night with congregation. The mean vectors $r_{n=62}$ and $r_{n=4}$ are shown as arrows whose length are drawn proportionally to the radius of the circle = 1. $n = 62$, $\alpha = 2°$, $r_{n=62} = 0.283$ ($p < 0.01$); $n = 4$, $\alpha = 315$, $r_{n=4} = 0.94$ ($p < 0.05$).

Because of the numerical problems outlined above it was decided to abandon weighting the respective nights, and to consider all nights as vectors of unit length (Fig. 1).

The distribution of all 62 nights proves to be non-uniform (Rayleigh test — see Batschelet 1965 — $p < 0.01$) and shows a highly significant clustering with respect to the hypothetical direction, the new moon (V-test — see Batschelet 1972 — $n = 62$; $u = 3.149$; $0.0001 < p(u) < 0.001$). The mean vector $r_{n=62}$ deviates by only 2° — this is equal to 4 hours past the new moon. The distribution of the 14 big nights is also significantly clustered with respect to the new moon (V-test: $0.01 < p(u) < 0.05$).

Around the 366 m Omege tower (North Dakota) congregations of birds without actual kills were observed on four nights (Avery et al. 1976), viz. Sept. 6—7, 1972; Aug. 22—23, Aug. 25—26 and Sept. 25—26, 1973, The circular distribution of the respective moon-ages (28, 24, 27, 28; see Fig. 1) also differs significantly from uniformity (Rayleigh test: $p < 0.05$), and shows a significant clustering with respect to the new moon (V-test: $n = 4$; $u = 2.08$; $0.01 < p(u) < 0.05$). The mean vector $r_{n=4}$ deviates at least three nights before the new moon.

Fig. 1 shows, moreover, that considerable bird mortalities at artificial lights have also been reported on nights long before or long after the new moon. I personally have found no reports about mortality on nights with moon-ages 13, 14, 15 und 16. In this connection it is worth noting that when there is a new moon there is no moonlight during the whole night. The waxing crescent leaves the second part of the night without moonlight because the moon goes down some time after sunset. The waning crescent on the other hand leaves the first part of the night without moonlight because the moon rises later in the night. It is only around full moon that no part of the night is without moonlight. Thus the period during which bird mortality occurred on a given night might be of interest. In most of the literature I have consulted the relevant data were too vague and scanty to permit even tentative conclusion to be drawn. The following example shows the potential significance of giving the detailed

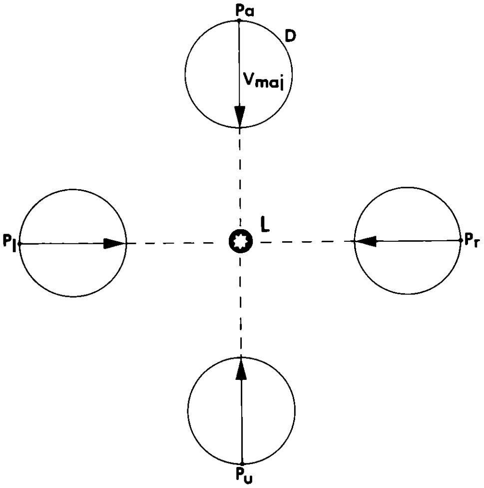

Fig. 2: Theoretical radiance-distribution diagrams in a vertical plane including the artificial light source L, and major vectors V_{maj} , at the points of observation Pa above, Pu under, and Pl and Pr besides L. Solid angle of acceptance of radiance detector 180° Arbitrary units. Reflection, scattering and absorption assumed to be zero.

timing of the kills. On the night of Sept. 9—10, 1948, birds had already been observed flying overhead for an hour when around midnight the first birds began to fall down the column of light of the ceilometer at Nashville airport (SPOFFORD 1949). The ceiling was 5000 ft, gradually lifting to 9700 ft at 4.30 a. m. when the last birds fell. By far the greater part of the 300 birds fell in the first hour when visiblility was 10 miles. Taking the lunar cycle into account I determined that the moon-age on this night was 5, and that this small crescent moon went down around 10.00 p. m., and thus no longer illuminated the cloud cover when the birds began to fall.

This example shows also that some factors frequently considered to be instrumental in kills, namely a low cloud ceiling and bad visibility, need not be crucial.

Some observations by CLARKE (1912) point in the same direction. In his voluminous work he argued first (Vol. I, p. 285): „When moisture is disseminated through the air as a liquid in a state of minute subdivision, the mixture becomes more or less opaque, and the powerful beams from the lantern then become conspicuous to a very remarkable degree, and exert extraordinary attractive powers over the migrants that pass within the sphere of their influence.“ In Vol II, p. 24, however, he specified the conditions as follows: „. . . the existence in the atmosphere of moisture not necessarily in the form of rain or haze, but actually present, though not visible, on dark starless nights“, and he stated „I have seen them (the birds) in great abundance at the lanterns when I could make out neighbouring lights that were ten miles or more distant . . . on the other hand, there was not a single instance of migrants visiting the light when the night was bright and starlit or the moon visible.“

3. Bird-Aircraft Collisions

The moon appears to be conspicuous by its absence in considerations and eyperiments about scaring bird out of the path of an airplane en route at night (review: LARKIN 1976; BLOKPOEL 1976). During aircraft surveillance of nocturnal migrants from a light aircraft cruising at an air speed of 120 mph, and equipped with auxillary landing lights, BELLROSE (1911) observed no tendency for small birds to be either attracted to or repelled by the lights. Small birds were seen to make only last-second dives to avoid the aircraft, but ducks and geese took evasive flight at much greater distances ahead of the aircraft, and only a few small birds were struck. During preliminary experiments at night with tracking radar LARKIN et al. (1975)

recorded three evasive manoeuvres of birds with respect to a small airplane with its landing lights on. In view of the kills at illuminated communication towers and at airport ceilometers the authors suggested that birds might also be attracted to the lights of an airplane. No data about the moon were given for the nights on which these experiments, and previous experiments with searchlights (Griffin et al. 1974) were carried out. The authors recommended an aircraft-mounted lamp projecting light focussed into a cone on the order of 3° in width aligned with the airplane's trajectory. Bird outside this cone would be unable to intersect the trajectory of the airplane as a result of the great difference in the airspeed of birds and airplanes. Blokpoel (1976) argued that on nights with poor visibility migrating birds might be attracted rather than repelled by aircraft-borne strobe-lights. Recently Yakobi (1978) expresses the view that birds are attracted by the landing lights of USSR civil aircraft, and are responsible for the frequent damage to these lights.

4. Discussion

It is widely held today that a combination of atmospheric „bad weather" conditions leads to kills among nocturnal migrant birds at tall lighted structures. The principle finding reported in the present paper is that these kills are also correlated with the lunar cycle. The evidence for this is to be found in a highly significant clustering around the new moon of bird kills on 62 nights in the USA between 1935 and 1973. This finding is in keeping with the effect that the phase of the moon has on the congretation of birds around lighthouses (Clarke 1912; Drost 1935; and others), and on the congregations of other animals (insects, fish) at artificial lights (Verheijen 1958, 1960, 1969; Ben Yami 1976). Light-traps catch fewer insects on nights with a full moon, although a greater portion of a given population may then be flying. This lunar periodicity in the catching of nocturnal insects by light-traps is much more marked in species which have their nocturnal activity round midnight than is species flying at dusk (Williams 1936). The probable reason is that the moon affects the angular radiance distribution in the vicinity of the lamp much more at midnight than at dusk (Verheijen 1968; for detailed discussions see Southwood 1971).

The moon appears to affect nocturnal bird migration in a complicated way that is not yet fully understood. Under laboratory conditions, with the level of illumination as the only variable, the amount of migratory restlessness in some caged nocturnal migrants is positively correlated with the illumination intensity over the range between new and full moon (Gwinner 1967; Czeschlik 1977). However, the visibility of the moon as a discrete source then seems to disturb the directional orientation of caged birds and thus disrupt their locomotor activity (Brown & Mewaldt 1968). Observations of nocturnal migrants in nature have led to contradictory conclusions: moonlight, or the moon, either influences migration in a positive or negative sense, or it does not influence it at all (Bretscher 1934; Dörr 1935; Nisbet & Drury 1968).

The common causal factor underlying the correlation of bird kills with both bad weather and with new moon might naively be termed bad visibility in the sense that under these conditions the obstructions are not readily seen. However, in the case of, for instance, a TV tower it is the tower itself and the guy wires that are not perceived, as can be deduced from the fact that most birds are injured or killed by striking these parts. The birds do perceive the warning lights because they have frequently been observed to congregate close to tower lights on overcast nights, whereas on clear nights they actively avoid such structures (Avery et al. 1976; cf. Clarke 1912 for detailed discussions relating to birds and lighthouses). Moreover, it has been observed that the number of birds seen close to a tower and the number of flight calls decreased when the tower lights were turned off, and incrased after the lights were turned on again (Cochran & Graber 1958; Avery et al. 1976). Brewer & Ellis (1957) reported that dead birds were often found lodged in the tower structure (Will-TV tower, Monticello, Ill.), but always in places away from the lights, and concluded, „at least at short range, the birds tended to avoid the lights rather than to seek them". In my opinion an alternative interpretation might be that the tower structure was illuminated in such a way that the birds could readily perceive and therefore avoid only the parts close to the lights, whereas parts of the structure further away from the lights were too weakly illuminated for them to be seen. Probably the birds were unable to perceive these dark parts because of the glare.

The combination of primary light sources — one or more lamps — and secondary light sources — a variety of obstructions — is characteristic for the conditions under which several species of animals are victimized during their nocturnal activities. The animals are killed deliberately by a variety of man-made entrapping obstructions accompanying the leight (a trap for insects and a net for fish) or accidentally by the obstructions which the light should warn them against (towers or airplanes in the case of nocturnal migrant birds). The lights of TV towers, lighthouses, and also airplanes, should warn human beings about some obstruction, not by increasing the conspicuity of the danger itself via illumination of the obstruction, but by appealing to the cognitive capability of men to associate (via more or less detailed and specific instructions) the in itself meaningless light with the danger. The fact that an obstruction is equipped with warning lights may frequently even mean that the obstruction becomes less perceptible because of glare.

For catching insects or fish with light the primary light source is frequently mounted in such a way that the trapping device is situated in the shade. Then almost nothing but the primary light source is visible (Verheijen 1958, 1960; Ben Yami 1971). Many aspects of the light source and the trapping device affect the species-specific approach-withdrawal balance, and therefore determine whether or not an animal is able to avoid collision or capture at the last moment (for insects see Southwood 1971). It can be assumed that the dangerous obstruction — at least when it is visible — presents sign stimuli which release and steer some protective reponse, for instance avoidance. If the anthropomorphic idea that a lamp might be an uncomfortably strong stimulus is discounted, then it is not really clear which aspects of „light" release protective behaviour (cf. Precht 1944).

The conclusion of Robinson & Robinson (1950) that „it is some special property of an isolated lamp which attracts insects" was confirmed for worker honey bees (*Apis mellifera*) and for the pike (*Esox lucius*) and the starling (*Sturnus vulgaris*) in my early experiments (for details see Verheijen 1958). Moreover I then put forward the hypothesis that this „trapping effect" of an isolated light source is the result of the unnatural angular radiance distribution in the vicinity of that light source. A similar suggestion with respect to planktonic organims came from Schallek (1943).

Before looking more closely at this hypothesis and at its relevance for nocturnal bird kills, I shall discuss some of the explanations for the congretation of birds and other animals at lights presented by other authors. The belief that animals are drawn to a light because they mistake it for a star, the moon or the sun has been expressed repeatedly, also with respect to bird kills (Kemper 1964). I have argued against this idea in general (Verheijen 1958), and Avery et al. (1976) maintained that such an explanation was unlikely as far as nocturnal migrant birds were concerned. A more sophisticated version of this idea was developed by von Buddenbrock (1917). He attributed the fact that insects fly towards a lamp to a compass reaction (menotaxis) to the near light source. Although this theory has been included ever since in almost every handbook on insect physiology it seems to me to be a very improbable explanation for the phenomenon. One of my arguments is that the animals can perform a sun-compass orientation by moving at a given angle between the longitudinal body axis and the parallel rays of light from the infinitely distant sun, until the information input from the environment calls for an adaptive change of this angle.

It is a complete mystery how the ability of an insect to adopt a suitable angle with respect to the rays of light should be restricted by a nearby light source in such a way that the insect adopts an angle which leads to its destruction (for an elaborate discussion see Verhejen 1958). The suggestion of Lorenz (1978: 183) that insects would also spiral away from a lamp, and that they would therefore not be observed by us, can hardly be taken seriously.

Detailed observations and suggestions have been made with respect to *Sardina* spp. fished with light in the Eastern Mediterranean and the Atlantic, such as: the fish are not attracted from a great distance but are trapped by the light after having drifted into the illuminated zone; they circle round the lamp or congregate down current from the light source (Le Men 1971; Ben Yami 1976). The observations also refer to marine invertebrates such as the worm *Platynereis dumerilii* (Verheijen 1958), nocturnal insects at light traps (Southwood 1971) and nocturnal migrant birds at lighted towers (Graber 1968; Avery et al. 1976); the wind affects flying animals in the same way as water current affects swimming animals. The diversified species-specific tricks applied by man for helping to protect animals from artificial lights, or, reversely, for perfecting the attracting power of artificial lights, should not conceal the fact that these tricks reflect universal behavioural aberrances under basically identical illumination conditions. The most extreme aberrance, hitting a light, is shown by birds when they are unable to perceive anything but this light, as is the case under overcast conditions when there is a new moon. Under improving illumination conditions the animals become less aberrant and they are able a) to avoid the primary light source but not the accompanying obstructions, so that they still may be victimized; b) to avoid both the light and the obstructions, although they still congregate; and, finally, c) to avoid the locality around the lighted obstruction so that statistically fewer animals are present than in similar localities without a lighted structure, as may occur in non-overcast conditions, with or without moonlight, or in complete overeast conditions when the overcast is moonlit.

Next I will argue that optic orientation system which allow for adaptative behaviour under natural illumination conditions may fail to cope with certain artificial illumination conditions which have a „trapping“ effect. The main idea is that an orientation system cannot be expected to represent a spatial environmental condition as a result of its evolutionary history, if this condition, because of its man-made character, did not present itself as an environmental pressure. Orientation systems based on sensitivity to radiation (light) can be divided roughly into two categories (see for instance SCHWERDTFEGER 1977):

1. photic systems attuned to scalar or vectorial features of the angular radiance distribution (ARD); and
2. visual systems attuned to configurational features.

The division into these two categories of orientation can be traced back in the literature in various directions. The biologist PRECHT (1944), for instance, distinguished Phototaxis (reaction to „light“) from Photoentaxis (reaction to „visible things“), whereas the psychologist GIBSON (1958) disputed the distinction between the ability of an animal to respond tropistically merely to light and its ability to respond to an object.

The difference between these two categories of orientation systems can be illustrated by the contribution they make to one and the same function, namely postural control in fish. Many species of free swimming fish tend to orient their dorsal side in the „direction of the light“ (VON HOLST 1935, 1948). In addition to this Dorsal Light Response (DLR), some species of fish show the tendency to orient their ventral side towards a visible substratum by means of the Ventral Substrate Response (VSR). The VSR is quite different from the DLR in several aspects e. g. the VSR is guided by configurational visual cues which represent a substrate, and it operates via a higher level of neural integration (MEYER et al. 1976; see also MEYER et al. 1979). The DLR and the VSR show that during active movements of several species of animals, invertebrates as well as vertebrates, the position of the body — or of parts of the body such as the head and/or the eyes — is to somer degree determined by spatial or directional information derived from the environment by sensory modalities that differ from the „vestibular“ one which use gravity (for a review see for instance SCHÖNE 1975).

I assume that the photic orientation system underlying the DLR is attuned to the natural egg-shaped form and „upright“ position of the radiance distribution solid (RDS), whose maximum irradiance vector, produced by downwelling irradiance, points in an upward direction (TYLER 1969; for spectral properties, which I do not consider here, see MUNZ & MCFARLAND 1977). Around an underwater lamp on a dark night the position of the RDS is only natural at measuring points under the lamp; elsewhere the RDS is tilted, because the maximum irradiance vector continually points towards the lamp. Irrespective of the reflection of light at the water surface the RDS is in an upside down position at measuring points above the lamp because the amount of upwelling irradiance overpowers the downwelling irradiance (Fig. 2). I suggest that this explains why sardine-like fish concentrate predominantly below an underwater lamp, a fact which is of extraordinary importance in fishing operations using light, for instance light-and-pump fishery (KURC 1969; LE MEN 1971; and others). Fish swimming beside and expecially above the lamp frequently behave in an agitated and capricious way which seems to indicate they are experiencing orientational difficulties.

In all probability a strong DLR also accounts for the similarly aberrant behaviour of insects flying near a lamp. There are to my knowledge only few data indicative of a DLR in birds. After one eye had been covered, a tilt of the head and the body was observed by SIMON (1954) in chicks of the domestic fowl. An animal could even turn over on its side with the uncovered eye directed upwards. The walking animal kep a straight course, whereas the flying animal flew in circles turning in the direction of the uncovered eye. The tendency of birds to congregate on dark nights below the level of tower lights might thus in part proceed as described above for fish.

Another effect of rotation around the longitudinal axis in flying and swimming animals might be that an animal which is tilted to the left because of the DLR with respect to a light to the left would automatically swing off to the left, thus circling the light. At least in birds and bats a turn is typically initiated by „banking" according to the principle of the banked turn (LIGHTHILL 1975).

Strong differences between the infux to the left and to the right eye also directly provoke turning in many species of animals. Elimination of the influx to one eye by covering it frequently results in circus movements, a phenomenon thought to be indicative of „tropotaxis" (for a critical evaluation see VERHEIJEN 1958; SCHÖNE 1975). It is conceivable that unnaturally large differences in the amount of excitation of sensory elements involved in photic orientation, induced by an RDS which has an unnatural shape (unnatural high Directivity, VERHEIJEN 1978, 1979) and position, will often provoke aberrant orientation — „disorientation" — if the error signals registered in the feedback control mechanism of the moving animal (cf. SCHÖNE 1975) acquire values beyond the range to which this mechanism is attuned.

Matt black paint is a widely applied finishing touch to apparatus for the study of phototaxis. It was, for instance, used by JAEGER & HAILMAN (1973) and HAILMAN & JAEGER 1976 (see also JAEGER 1978) in studies of phototaxis in Anura. According to their hypothesis the function of phototaxis in frogs is to find a species-specific optimum ambient illumination. This hypothesis is based an the — partly forced — choice between two stimuli in an apparatus with a starting box painted matt black. BOYCOTT et al. (1964) found, however, that painting the starting box matt white affected the animal's choices in that more „negative" responses were scored. This was attributed to the difference in the level of illumination in the „light" as opposed to the „dark" starting box (see also MUNTZ 1977). I suggest that the different Directivities of the ARD's in the white and in the black walled starting boxes might be another, and perhaps more powerful, factor underlying the differences in response.

Visual orientation systems are attuned to configurational features of the environment. Therefore the eyes must reproduce or image the environment in some detail. In general the visual world is sampled more densely in some parts of an eye than in others. For this purpose one or more regions of an eye termed „area" are characterized by showing a smaller angle between adjacent receptors. In birds with laterally situated eyes the central area of each eye is stimulated by stimuli in the monocular ipsilateral visual field (MEYER 1977). A similar situation exists in many species of fish (ALI & ANCTIL 1976) and insects (HORRIDGE 1977). Movements of one or both eyes, of the head or the whole body (depending on the degree of mobility of the eyes and the head of the animal concerned) can cause any region of the environment to be imaged on an area of the eye.

A large amount of literature about this orienting respense — the visual grasp reflex — has accumulated. The response can be released not only by visual stimuli, but also by electrical stimulation of central nervous structures. There are indications that in the latter case the absence or presence of „appropriate sensory cues" or the „organization of the environment" determine whether the response turns out to be an isolated, stereotyped output, or is part of a more complex and purposeful behaviour pattern (see for instance PHILIPS & YOUNGREN 1971).

Using a method of PRECHT (1944), BAUERS (1953) demonstrated that walking worker honey bees try to turn towards a lamp in such a way that the frontal ommatidia are stimulated, and then they try to proceed towards the light source. I showed (VERHEIJEN 1958) that these insects may then be unable to avoid being scorched by a 500 watt incandescent lamp. Recently it was found that restrained Barbary doves (*Streptopelia risoria*) oriented their bead towards a lamp placed in various positions so that they fixated it monocularly with the central area (ERICHSEN 1977; see also BLOUGH 1971; CATANIA 1964; NYE 1973). In fish the visual grasp reflex has been evoked by central stimulation (AKERT 1949) and by stimulation with a light source (VERHEIJEN 1958). Essential information with respect to both the releasing stimuli and the neuronal circuits involved in the visual grasp reflex, has been obtained in man, when in a healthy condition and when showing certain syndromes resulting from brain damage (for a comparison of data, concepts, and theories in ethology, psychology and psychiatry see PLOOG 1964). During prolonged observation of a picture fixations of the human eye appear to concentrate on two types of regions characterized by „contrast" and by „meaning" respectively (YARBUS 1967). In man ENGEL (1976, 1977) found involuntary fixations of configurationally non-targets because of contrasts as well as voluntary fixations of targets because of their configuration. Therefore he introduced the concepts of visual conspicuity and cognitive conspicuity. With respect to the stimulus situation visual and cognitive conspicuity refer to the factors „contrast“ and „configuration“ respectively, and the eye movements towards these two types of stimuli would be controlled at an early and low or at a late and high level of neural processing. There are indications that in man the direction of eye movements can even be controlled at a neural level which does not require observable stimuli: PÖPPEL et al. (1973), for instance, reported that patients with a cortically blind area in the field of vision can perform a saccadic eye movement directed towards a 100 ms flash located within the blind area: they would „look“ in the direction of an invisible target.

In predators, visual fixation of — „looking at“ — a stimulus can lead to prex catching or to flight (approach or withdrawal, SCHNEIRLA 1965). The dimension, shape and movement of a stimulus determine which of these two behaviour patterns will be released. This has been studied extensively and at length in toads (EWERT 1974). After thalamus/pretectal lesions toads are no longer able to distinguish visual patterns in a behaviourally relevant manner: prey-catching is disinhibited, and the key stimulus „prey“ is reduced to „being visible“ or „showing contrast“ (EWERT 1976; EWERT & VON WIETERSHEIM 1974; see also discussion by SCHÖNE 1975 and MUNTZ 1977). According to the concepts of ENGEL (1976, 1977) prey-catching now occurs in response to stimuli showing only visual conspicuity.

For the rhesus monkey KLÜVER & BUCY (1939) described a syndrome with a polysymptomatic expression following bitemporal lobectomies. One symptom of this KLÜVER-BUCY syndrome was termed „hypermetamorphosis“: there is a compulsive tendency to orient visually to everything in sight, to approach it and to touch it. The syndrome is a rare occurrence in man. It has been analysed in detail by PILLERI (1966), and it was recently described in a female patient (SHRABERG & WEISBERG 1978). Similar symptoms occur during ontogeny in children and can reappear as a result of cerebral dissolution, for instance in senility (Jackson 1884). KRETSCHMER (1940) called the state of blockage of all higher cerebral functions resulting in the appearance of the autonomic functions of the brainstem the „apallic syndrome“. The symptomatology of chronic mercury poisoning can progress to the apallic syndrome and death. This was seen in Japan in the sixties in the case of the notorious Minamata disease which was caused by people eating fish, especially shellfish, contaminated with industrial effluent (see for instance TAKEUCHI & ETO 1976). Recently, symptoms of the KLÜVER-BUCY syndrome (optic fixation, object-mouth approach) were observed in Iraq in patiens who had eaten wheat preserved with a mercury compound (GERSTENBRAND et al. 1977). Obvionsly the sign-stimuli for the approach response of the KLÜVER-BUCY syndrome are also reduced to visual conspicuity.

I now return to the subject of bird kills. The visual orientation system of a bird flying in complete darkness in the vicinity of an artificial light source might fail to cope with the trapping situation as follows. Because of its visual conspicuity the light source will be imaged on the area, or on one of the areas, by the orienting reflex. If the light source is imaged on the temporal areas of both eyes, then the bird will fly straight towards the light source. If it is imaged on the central area of, for instance, the right eye, then the bird will start circling, keeping the light source to the right. Differences in the refractive power of the eye — or its accomodative ability — in different directions (the pigeon was found to be short-sighted in the anterior visual field and long-sighted in the lateral visual field: CATANIA 1964) might play a role in these phenomena. Because the light source is not cognitively conspicuous, and because the dark environment does not produce such stimuli, partly owing to the glare, the higher levels of neural integration that should decide to stop this behaviour are left without information about the dangerous character of the situation. Thus the behaviour can proceed in a stereotyped „forced“ way as is shown by organisms with central defects similar to those leading to the apallic syndrome in man.

It can hardly be pure accident that most species of fish caught with light in commercially valuable quantities (BEN YAMI 1976) show pronounced and stable schooling behaviour. Although it is now well documented that schooling in fish — and similarly flocking in birds — increases the efficiency of food finding and protection from predators (for reviews see WILSON 1975; KREBS & DAVIES 1978) the causal mechanisms leading to the various forms of schooling and flocking are not yet well understood. Anyway it would seem that mutual attraction and social facilitation together with the necessity for avoiding collisions between members play in important role in releasing and steering these animal groupings. Compensation of shifts in parameters derived from the animal's visual perception of each other would lead to both sensory and motoric space constancy. The phenomenon „milling“ strongly resembles the circling of animal congregated around a light. The causal factors involved in milling might also be operative in congregations round a light. In a review of his extensive studies of fish schooling BREDER (1959) stated that „the production of a mill is most likely the result of some more than usually strong influence which exerted in less degree would produce other movements with utilitarian uses which at this time no one has been able to ascribe to a mill". Mass panic frequently seems to increase or intensify schooling and milling under natural conditions as well as in congregations around artificial light. The artificial light source might provoke milling-like behaviour by the panic-inducing failure of the photic and visual orientation systems, and in addition the source might determine the milling centre, because, while milling around the lamp, fish and birds might statistically keep the image of the lamp at the central fovea of one eye.

The inevitable conclusion from the above considerations seems to be that both the photic and the visual orientation system may fail to cope with the unnatural ARD around an artificial light source (trapping effect: VERHEIJEN 1958, 1960, 1969). We would do well to realize that we run the risk of overestimating the level of integration, and, inevitably, of misinterpreting the biological consequences of the activities of an animal under artificial illumination conditions. Thus the frequently given facile explanation that an animal approaches „the light" under artificial illumination conditions because it is „positively phototactic" too easily assumes an internal state of the animal directly or indirectly related to some optimum „light intensity", and driving an optimal behaviour. The far from beneficial outcome — the animal being injured, scorched or crushed — emphasizes the aberrant character of the reaction.

The reliability of the use of a vertical ceilometer light beam in studies of low altitude nocturnal bird migration has been estimated by comparing the results of this method with those of simultaneous moon watching (ABLE & GAUTHREAUX 1975; GAUTHREAUX 1979). This comparison is impossible with a new moon, or when the moon is below the horizon. Under overcast conditions however the ceilometer might then produce misleading data about the intensity and the direction of migration because of the trapping effect of the light beam.

Relatively little systematic research has been done in connection with the reduction or elimination of nocturnal bird kills at obstacles with lights and at airplanes. Success has been achieved by interrupting the trapping stimulus situation, replacing the stationary ceilometer by the rotating beam ceilometer, and replacing the stationary warning lights on tall obstacles by lights of the strobe or flashing type. Differences in the effect of flootlighting obstacles (AVERY et al. 1976) might be attributed to the direction and the degree of divergence of the beam. Broad beams directed downwards at an obstacle, which is often accompanied by a general site illumination, might reduce the directivity of the light field, and thus reduce the trapping effect, whereas a narrow beam directed upwards, and partly shining past the obstacle, might for birds flying above the obstacle produce an upside-down RDS with a high directivity, thus adding to the trapping effect of the obstacle's warning light.

In view of the fact that bird kills occur frequently at night at obstacles equipped with a light or a light beam it seems highly illogical that lights or light beams should be mounted on aircraft to scare birds out of the path of aircraft en route at night. However, a narrow beam might prove to be a more promising scaring device than is suggested by the above considerations about the factors underlying the trapping effect of artificial light. A bird in the narrow zone of collision in front of an aircraft approaching at high speed might move from this zone if the animal reacted with an undirected startle response upon being stimulated suddenly by the aircraft-mounted narrow beam. Of course an evasive manoeuvre would be even more successful, as was correctly suggested by GRIFFIN et al. (1974) and LARKIN (1976).

It is a serious problem in evaluating reports of nocturnal bird kills and accounts of experiments designed to reduce these kills, that generally practically no data are given about an essential factor, the moon, Therefore I recommend that, in addition to the almost omnipresent atmospheric data, reports on bird kills should include relevant data about the moon (position above the horizon, phase).

A natural ARD is an orientational requirement for the survival of many animals. This was shown with respect to the negative phototaxis of the seawater wetted sand-hopper *Talitrus saltator* (VERHEIJEN 1978), and the positive phototaxis of hatchling sea turtles (VERHEIJEN & WILDSCHUT 1973; VAN RHIJN 1979). A natural ARD was the starting point for the successful design of bee flight rooms at our laboratory (VAN PRAAGH 1972). The introduction of an artificial light source in nature frequently results in the destruction of the natural ARD as an orientational requirement. I propose that the term photopollution be used to denote the environmental hazards associated with the introduction of artificial light in nature. Basically the hazards of photopollution show a complex rhythmicity resulting from the activity rhythm of the potential victim on the one hand, and the lunar rhythm of the occurence of the trapping light field conditions on the other hand. The noisy effect of atmospheric conditions on both the victim's acitivity and the trapping light field conditions may obscure the lunar rhythmicity to such a degree that, without adequate statistical analysis of dates, the lunar periodicity of kills at artificial lights has not been noticed, or, has even been refuted. It would seem that an environmental impact assessment of photopollution is urgently needed.

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5. Abstract

Reports of bird kills resulting from collisions with tall lighted structures and with aircraft usually give data about the meteorological conditions, but hardly ever about the moon. The dates of 62 nights on which birds were reported killed at tall lighted structures in the USA between 1935 and 1973 are considered as if they were a sample of a circular distribution of nights in a lunar month. This distribution proves to be non-uniform with a highly significant clustering around the hypothetical direction, namely the new moon. It is suggested that the occurrence of mid-air bird/airplane collisions at night may show a similar relation to the phase of the moon. The effect of the moon is explained by assuming that even under overcast conditions moonlight reduces the unnatural anisotropy of the light field produced by an artificial light source, thus reducing the degree of disorganization of a bird's photic and visual orientation systems. Possibile reasons why these orientation system fail to cope with an artificial light source are discussed in detail.

6. Zusammenfassung

Der Mond: ein unberücksichtigter Faktor in Studien über Kollisionen von nächtlich ziehenden Vögeln mit hohen erleuchteten Hindernissen und mit Flugzeugen.

Berichte über Kollisionen von Vögeln mit hohen erleuchteten Hindernissen (Fernsehsendern u.s.w.) und mit Flugzeugen enthalten in der Regel Einzelheiten über die jeweiligen meteorologischen Bedingungen, während Angaben über den Mond fast stets fehlen. Die Daten von 62 Nächten zwischen 1935 und 1973, für die Berichte über an hohen erleuchteten Hindernissen in den USA getötete Vögel vorliegen, wurden als Kreisverteilung über die Lunarperiode (Mond-Monat) aufgetragen. Die Verteilung erweist sich als nicht-gleichförmig und zeigt eine hochsignifikante Häufung von Werten um die hypothetische Erwartungsrichtung an, nämlich um die Neumond-Phase. Es wird vermutet, daß das Auftreten von nächtlichen Vogel-Flugzeug-Kollisionen eine ähnliche Beziehung zur Mondphase aufweist. Dieser Mond-Effekt wird durch die Annahme erklärt, daß das Mondlicht — auch unter bedecktem Himmel — die unnatürliche Anisotropie des Lichtfeldes abschwächt, das von einer künstlichen Lichtquelle ausgeht, und damit den Grad der Desorganisation in den photischen und visuellen Orientierungssystemen des Vogels vermindert. Es wird eingehend erörtert, weshalb diese Orientierungssysteme einer künstlichen Lichtquelle nicht gewachsen sind.

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Biologie des Eleonorenfalken (*Falco eleonorae*)
9. Eitemperaturen und Körpertemperatur juveniler und adulter Falken während der Brutzeit

Von Michael Wink, Coralie Wink und Dietrich Ristow

1. Einleitung

Der Eleonorenfalke brütet im Hochsommer auf vegetationsarmen Felseninseln des Mittelmeeres. Seine Horste befinden sich auf dem Boden und sind im Tagesverlauf zumindest zeitweilig der intensiven Sonneneinstrahlung ausgesetzt. Zur Untersuchung der Brutbiologie unter den halbwüstenhaften Bedingungen des Brutplatzes bestimmten wir Ei- bzw. Bebrütungstemperaturen, die Entwicklung der Thermoregulation bei den Jungfalken sowie die Körpertemperatur der Altfalken in einer ägäischen Brutkolonie.

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2. Material und Methode

Die Rektaltemperatur T_b juveniler und adulter Falken wurde mit einem geeichten Quecksilberthermometer gemessen (Genauigkeit 0,1° C). Die am Tage gefangenen Altfalken wurden vor der Messung 15 Minuten lang im Dunkeln ruhig gehalten; Jungfalken wurden sofort untersucht. Bei der telemetrischen Temperaturbestimmung mittels Kleinstsender (Ellis 1973) wurde der Sendefrequenz eine Taktfrequenz aufmoduliert, die der Temperatur proportional war (Genauigkeit ca. 0,1° C). Durch mehrere Ringe aus Kupferdraht um den Horst und einer 5 m langen Antenne wurde die Richtwirkung der Sender verbessert, so daß unter optimalen Bedingungen die Taktfrequenz mehr als 30 m entfernt digital registriert werden konnte. Zum Teil wurden die Signale jedoch in einem 6 m entfernten Tarnzelt aufgenommen, um gleichzeitig Details der Brutaktivität beobachten zu können.

Da ein zwischen die Eier gelegter Sender vom Falken-♀ sofort entfernt wird, wurde zur Ermittlung der Eitemperaturen T_e der Sender mit Silikonfett und Paraffin wasserdicht versiegelt und in ein kleines, braunes ausgeblasenes Hühnerei eingebaut. Dieses Meßei wurde vollständig mit Wasser gefüllt — um ähnliche Bedingungen wie in einem natürlichen Ei zu schaffen — und mit einer Folie verschlossen. Wenn wir das Ei zu anderen Eiern in einen Horst legten, wurde das Gelege von den Falken sofort wieder bebrütet — selbst bei künstlichen 4er-Gelegen.

Zur Registrierung der Hauttemperatur T_s wurde der Sender (Gewicht einschließlich Batterie 2,3 g) mit Branding Cement unter den Achseln eines Jungfalken befestigt. Referenzsender für die Umgebungstemperatur T_a wurden in unmittelbarer Horstnähe befestigt, so daß gleiche Sonnen- und Winderexpositionen wie im Horst vorlagen. Zur gleichzeitigen Überwachung von T_e bzw. T_s und T_a wurden Sender mit unterschiedlicher Sendefrequenz verwendet.

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