MODIFICATION OF MAMMALIAN SEXUAL CYCLES

IV. DELAY OF OESTRUS AND INDUCTION OF ANOESTRUS IN FEMALE FERRETS BY REDUCTION OF INTENSITY AND DURATION OF DAILY LIGHT PERIODS IN THE NORMAL OESTROUS SEASON[1]

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INTRODUCTION.

Recent experiments with ferrets of both sexes have shown conclusively that the seasonal sexual cycles of these animals can be modified considerably and even reversed by changes in the daily duration and intensity of the light to which they are exposed (Bissonnette, 1932 *a*, *b*, 1933 *a*, *b*, 1934 *a*, *b*, 1935 *a*, *b*; Hill and Parkes, 1933 *a*, *b*, 1934; Allanson, Rowlands and Parkes, 1934; Marshall and Bowden, 1934; and others cited by them). Pseudo-pregnancies have been induced in November, December, and January; real pregnancies as early as December 29th and January 1st, giving litters of nine and ten young on February 8th and 11th (Allanson, Rowlands and Parkes, 1934), whereas, under natural seasonal light cycles, these animals mate only between March 1st and September 1st (Allanson, 1932; Hammond and Marshall, 1930).

Rowan's (1925, 1926, 1928, 1929, 1930) studies on Juncos, crows and canaries, and Bissonnette's (1933 *a*, *b*, and previous papers) on starlings, in this connection, had already shown that their sexual cycles were susceptible of modification by changes in light cycles, though Rowan considers that longer exercise periods, either with or without light, directly cause the sexual changes in birds. Bissonnette's studies indicate that, in starlings at least, changes of lighting, *per se*, are the primary modifying factors, though diet may act as a limiting factor. Cole's (1933) study on mourning doves, which breed in captivity, supplemented Bissonnette's on starlings and showed that fertility and viable eggs and sperms can be obtained out of normal season in that species by the methods of Bissonnette and Rowan by altering the light cycles by increased daily lighting in autumn after dark.

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Baker and Ranson (1932 *a*, *b*, 1933) have also shown that the seasonal sexual cycles of voles can be modified in like manner, though food and locality modify the response.

Poultrymen generally have taken advantage of this phenomenon to increase autumn and winter egg production by night lighting.

However, the studies of Young and his students (Dempsey, Myers, Young and Dennison, 1934) have shown that the polyoestrous cycles of guinea-pigs are little, if any, modified by alterations in light cycles or even by almost complete darkness, except to change slightly the average time at night when females first show receptivity to the male. The well-known fact that sheep and some other animals come into oestrus in autumn, the failure of Moore's students (Wells, 1934; Moore, Simmons, Wells, Zalesky and Nelson, 1934) to induce any changes in seasonal sexual cycles of the thirteen-lined spermophile by changes in seasonal light cycles, the breeding habits of many tropical birds in Africa, with breeding seasons throughout the year or coming in relation to wet and dry seasons either once or twice a year (Marshall and Bowden, 1934; Bissonnette, 1932 *b*; and others cited by them) indicate that this sexual photoperiodism is not a universally uniform phenomenon and that different species have each its genetic peculiarities in respect to the relations of its breeding mechanism to environmental factors such as light, food, temperature, available nest-forming materials, etc.

In ferrets, at least, it has been shown rather conclusively that the anterior lobe of the hypophysis is concerned in sexual photoperiodism (Bissonnette, 1932 *a*, 1933, 1934 *a*, *b*, 1935 *a*, *b*; Hill and Parkes, 1933 *a*, *b*), since hypophysectomised animals go into permanent anoestrus or spermatogenic and interstitial cell infantilism or atrophy and are unaffected by night lighting, but are affected by injections of some anterior lobe hormones as are other animals.

Bissonnette and Rowan (in papers cited above) have both shown that reduction of lighting for the birds used by them induced sexual regression in both males and females, already either completely or partially activated sexually.

Hill and Parkes (1934) found that reduction of the day length to $\frac{1}{2}$ hour or less of light per day, beginning January 24th, after normally increasing day length for the 34 days from December 21st, did not prevent either males or females (with one exception) from coming into sexual activity, producing young, and again coming into oestrus, within the $5\frac{1}{2}$ months of their experiments. However, as Marshall and Bowden (1934) and Bissonnette (1935 *a*, *b*) have pointed out, the oestrus of the females, at least, was considerably delayed. Their conclusions that the reduced lighting did not prevent "normal" oestrus in their animals and that reduced lighting does not modify the normal seasonal sexual activity in spring seem to be too sweeping in view of the delay of the beginning of the experiment for 34 days of normally increasing day length, which is known to be sexually activating from their own experiments as well as from those of Bissonnette *et al.*

It, therefore, appears pertinent to the general problem to report some of our results in this connection, particularly as Hill and Parkes pass them over as "not conclusive", as well as those pertaining to the induction of anoestrus in fully or

partially oestrous females by reduction of either duration or intensity of the light to which they are exposed daily.

MATERIAL AND METHODS.

(1) *Using curtains.*

Female ferrets, Nos. 3*c*, 4*c*, 6*c* (white) and 5*c* (black), were exposed to normal day lengths in the animal house at the Institute of Animal Nutrition, Cambridge, England, from December 15th to January 16th. They were then curtained from 4 or 4.30 p.m. till 9 or 9.30 a.m. each day till April 14th, after which time the curtain was drawn from 3 p.m. till 10 a.m. daily. The cages were so arranged that they faced one large group of windows and had another window facing across their fronts from the right end of the row of cages. The cages, therefore, received light from in front and from the right side. The curtain was so arranged that it slid by a guide wire across the fronts of all cages from left to right, but was not turned back around the cages at the right end. This led to somewhat greater lighting in the cages nearest the right end of the rows of cages and deep darkness in the cages to the left, whenever the curtain was drawn. This was enough to make a difference in the rates at which the animals were sexually activated, those in the cages to the right preceding those in the darker cages to the left.

No. 3*c* was killed on March 4th, No. 4*c* on May 19th (27 hours after the beginning of a normal copulation), No. 5*c* on May 20th (44½ hours after the finish of a copulation), and No. 6*c* on May 19th. For controls females 7*c* and K were bought on March 1st and 7*c* killed on the 4th. K was curtained with the rest from March 1st till she was killed on May 12th.

No. 3*c* was in one of the left cages, No. 4*c* near the right (lighter) end and was moved over to the left end on April 25th when her vulva was swelled to about three-quarters maximum size. No. 5*c* was also in the lighter cages till April 11th and moved to a darker cage when her vulva was about half swelled. No. 6*c* was treated like No. 5*c*, but was only one-third swelled on April 25th. Female K was not moved but was at the darker end from the start.

(2) *By reduction of lighting periods.*

In addition, some females, G, C, B, that had been undergoing experimental lighting of 6½ hours after normal days from December 7th till February 22nd or longer, 6 hours till April 14th, 5 hours till May 5th and 4 hours thereafter, were found to come into complete or partial anoestrus as a result of the reduced duration of day length even at the higher level of daily exposures. Females D and A were transferred from the "long-day" schedule of lighting, just described, to the short-day schedule, behind the curtain, on April 18th and so cut from about 19 hours of light per day to about 5 hours.

The light and sexual histories of all these females are summarised in Table I. Sexual histories of controls are not given, as they remained in oestrus till mated or till killed for comparison. The females described by Hammond and Marshall

(1930) may also be taken as controls, as they were kept under normal conditions in these same animal houses or in similar ones as described by them.

(3) *Using hoods.*

In addition to the evidence from the ferrets described above it was noticed in other experiments, where hoods were used to prevent light reception by the eyes, that, if animals were getting their hoods off for part of the scheduled hooding time, they came into oestrus slowly. But if the hoods were put on again for part of the day to make up for the unscheduled lighting, the females went out of oestrus, to return to it later when the light time per day was again lengthened. These experiments are described elsewhere from another standpoint. But data relating to the effects of shortening days by hooding upon animals either fully in oestrus or partially activated is given here as corroborative evidence.

Female No. 1*c* was hooded from March 4th onward at Cambridge, England, daily from 4.30 p.m. till 9.30 a.m. till April 14th, then from 3 p.m. to 10 a.m. and received the light of normal days + 6 hours of electric light to April 14th, then 5 hours till May 5th, and 4 hours thereafter to May 18th. Before April 10th, she got the habit of removing the hood occasionally in the mornings and began to show first signs of vulval swelling on April 9th; reached one-third maximal swelling on April 21st; then, on reduction of lighting time and increase of hooding time per day, her vulva shrunk to about one-sixth maximum size by April 23rd. After this time she got the hood off fairly regularly in the early mornings and came into full oestrus before May 18th, when she was mated.

In contrast, female No. 2*c*, hooded in like manner, but failing to get the hood off at all frequently, did not come into oestrus at all till she died on May 8th from tuberculosis, which disease, in other cases, did not of itself prevent light induction of oestrus, and pregnancy, even within 25 days of death from the disease. In her case hooding was completely effective in preventing oestrus even with strong experimental lighting before May.

It is significant in this connection that female 1*c* underwent regression when hooding time was increased or when lighting time was cut down or under both changes acting together, though decreased lighting time with decreased hooding time after April 23rd induced or permitted complete oestrus.

Similar experiments with hoods in Hartford, in which similar habits of working hoods off in the morning hours developed, led to oestrous swelling, followed by regression when hoods were put on for 3 hours each day they were found off in the morning.

Female 1*h*, hooded daily from 4.30 p.m. to 8.30 a.m., with 6 hours of electric light per night beginning on November 10th, got the habit of getting her hood off on an average of about one night in four till March 15th, after which date the hoods were put on again for 3 hours each forenoon whenever they were off in the morning. She showed the first vulval swelling on March 11th, reached full swelling on March 20th–April 3rd and regressed fully before April 28th and remained in that condition till May 9th, when hoods were removed altogether.

Her vulva began to swell on May 29th and reached full size before June 8th, when she was mated and ovulated within 35 hours of the finish of copulation.

Female 3*h*, similarly treated, but getting the hood off very infrequently, did not show first signs of vulval swelling till April 3rd. She was accidentally poisoned with sodium fluoride on April 7th, not yet fully in oestrus.

DISCUSSION.

The sexual histories of all the above-described animals show that increases of either duration or intensity of daily illumination lead to increased sexual activity and eventually to complete oestrus. They also show that reduction in either intensity or duration of such lighting leads to sexual regression or anoestrus or retards the induction of oestrous activity. This regression may be induced in animals at complete oestrus or in those nearing that condition. They therefore indicate unmistakably that seasonal sexual cycles in female ferrets are conditioned to a considerable degree by their light cycles and may be modified in either direction by changes in the normal seasonal light cycle in different localities.

These results are consistent with the findings of Marshall and Bowden (1934), with our own, with those of Allanson, Rowlands and Parkes (1934), and with most of the studies of Hill and Parkes (1930–4). If, as may be suspected, the animals of Hill and Parkes (1934), receiving only one half-hour or less per day of light, were already well stimulated toward sexual activity in the 34 days of normally increasing days before January 24th, and merely continued to come into sexual activity but at a retarded rate, as appears from their data, and even returned to oestrus following gestation and suckling on a reduced light schedule to which they had become acclimatised, then the whole of the data are consistent. And they indicate that in ferrets any inherent rhythm of sexual activity or cycle is modifiable by changes in the light cycles to which the animals are exposed, and is so modified in nature by the normal seasonal light cycle.

Marshall and Bowden (1934) show that differences in intensity of light modify the reactions of the ferrets to night lighting rather than differences in wave-length. As Bissonnette (1932 *a*, *b*) showed, both intensity and wave-length were factors in the effectiveness of added illumination with starlings. These findings point to species differences in the relation of sexual cycles to light cycles in animals, as has been discussed elsewhere in another connection.

SUMMARY.

1. Cases are given in which female ferrets, already coming into, or in, oestrus as the result of artificially increased lighting in winter and spring, underwent regression or were retarded in their activation by reduction of either intensity or duration of daily illumination.

2. In some cases activation was resumed when light time or intensity was increased again.

3. These results are taken to indicate that, in female ferrets, any inherent rhythm or cycle of sexual activity is modified either naturally or artificially by

changes of the cycles of duration and intensity of the light to which they are exposed daily, and so made to correspond in phases with the seasons, or changed therefrom. The rising daily illumination in spring and the falling one in late summer and autumn probably accelerate and retard the sexual activity of the female ferret, or accelerate the onset of anoestrus in late summer and autumn.

4. The data on modification of sexual cycles or activity in ferrets, so far obtained, are consistent with these conclusions.

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Table I.

No. of ferret	Light history	First swelling of vulva	Later changes in vulva	Changes in light history	Response to light changes	Mated	Pregnant or pseudo-pregnant	Killed	Remarks
7*c*	Bought Mar. 1; normal light. Control, reference	—	—	—	—	—	—	Mar. 4	Uterus congested; vagina enlarging; vulva still showing no sign
K	Bought Mar. 1; curtained 4 or 4.30 p.m. to 9–9.30 a.m. daily, till April 14; 3 p.m. to 10 a.m. to May 12	April 5	Fully swelled April 23	None	—	April 27, 28	P.	May 12	Pregnant 14 days; vulva going down; in darker cage
3*c*	Normal days, Dec. 15–Jan. 16, then curtained as for K till Mar. 4. In a darker cage	—	—	—	—	—	—	Mar. 4	Reproductive tract small and in winter condition; not like No. 7*c* above
4*c*	As for K above till May 19, but moved to left of cages	Mar. 31	½ up April 23	Moved to darker cage, April 25	Swelling down to ½ size then back fully up May 9	May 18	—	May 19	Killed 27 hours post-coitus (beginning); no ovulation yet
5*c*	As above till May 20, but moved to darker cage April 11	Mar. 31	½ up April 11	Moved to darker cage, April 11	Vulva shrunk till May 6; up fully May 15	May 18	P.	May 20	Killed 44½ hours after finish of mating; eggs in tubes in pronuclear stages; granulosa cells off the egg
6*c*	As for 5*c* above	April 18	½ up April 25	As above	Vulva fully down	—	—	May 19	Delayed in onset of swelling; then regressed, to winter condition as result of reduced light
G	Normal day+6½ hours electric light, Dec. 7–Feb. 22; 6 hours to April 14; 5 hours to May 5; then 4 hours	—	Fully up Feb. 17. ½ up on April 21 a second time	Reduced 1 hour on April 14; May 5	Regressed completely before May 9	Feb. 17, 18	pP.	May 9	After coming partly into oestrus after a pseudo-pregnancy in April, she underwent regression on reduction of daily light even though this was still greater than is normal for the season
B	Normal day+added electric light as above for G; but starting in October	Nov. and Jan.	Fully up Nov. and Jan. and on Mar. 21 40 days after pP ended	As for G	Still up on April 23; but went well down by May 17	In Dec. and Jan.	pP.	May 17	Underwent regression as result of light reduction during the period of normal oestrus even though day length is above normal for the season
C	As for G	—	Feb. 16	As for G	Did not come on heat at all after light reduction	Feb. 16	pP. till Mar 30	May 18	She failed to come into oestrus again in April after end of pseudo-pregnancy as is usual at the season; result of reduction of lighting
D	As for G till April 18; then transferred to short days of about 5 hours per day	—	Fully up Jan 30 after 54 days lighting. ½ up on April 18	April 18 moved to 5-hour day	Went down from April 23 till fully down on May 20	Jan 30	pP.	May 20	Underwent full regression on reduction of the light in the normal oestrous season
A (cataract in 1 eye)	As for B till April 18; then moved to the 5-hour day	—	Nov. 23 after 42 days light. Feb. 12, 22 days after pP, and on April 18	Reduced light 1 hour on April 14; moved to 5-hour day from one of about 19 hours on April 18	Went to mid-winter condition between April 18 and May 9	Dec. 10, Feb. 12	pP.	May 20	Anoestrus again induced by reduction of light in the normal oestrous season

N.B. P. = pregnant; pP. = pseudo-pregnant.