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Prior Experience with Photostimulation Enhances Photo-Induced Reproductive Development in Female European Starlings: A Possible Basis for the Age-Related Increase in Avian Reproductive Performance[1]

Keith W. Sockman,[2,3] Tony D. Williams,[4] Alistair Dawson,[5] and Gregory F. Ball[3]

Department of Psychological and Brain Sciences,[3] Johns Hopkins University, Baltimore, Maryland 21218
Department of Biological Sciences,[4] Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6
Centre for Ecology and Hydrology,[5] Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, United Kingdom

ABSTRACT

Reproductive performance in female birds improves with age, and this is generally attributed to experiences obtained during breeding. In temperate-zone species, experience with photostimulation during the first breeding year may prime the hypothalamo-pituitary-gonadal axis to respond to photic cues more rapidly or robustly in subsequent years. To test this idea, we captured 32 photorefractory juvenile (hence naive to photostimulation) female European starlings (*Sturnus vulgaris*) and held half of them (naive group) on a photoperiod of 8L:16D for 32 wk and the other half (experienced group) on 8L:16D for 12 wk, 16L:8D for 12 wk, and then 8L:16D for 8 wk. When we subsequently transferred all birds to 16L:8D, the increase in body mass, which may presage egg laying in the wild, was more robust in experienced than in naive females. Experienced females also showed a more robust elevation in plasma concentrations of the yolk-precursor protein vitellogenin, although naive females showed an initial rapid but transient rise in vitellogenin that we attribute to their extended exposure to short-day photoperiods prior to photostimulation. Finally, the photo-induced increase in diameter of the largest ovarian follicle, in plasma concentrations of luteinizing hormone, and in the number of septo-preoptic fibers relative to the number of cell bodies immunoreactive to GnRH was greater in experienced than in naive females. Thus, prior experience with photostimulation enhances some initial phases of photo-induced reproductive development and may explain, in part, why reproductive performance improves with age in temperate-zone

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INTRODUCTION

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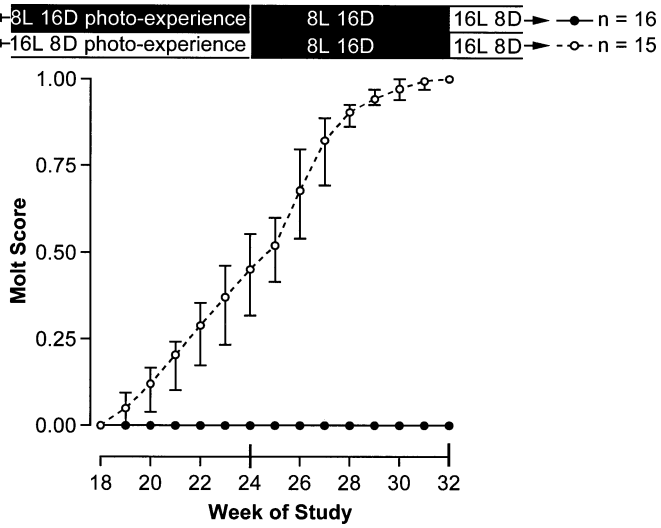


FIG. 1. Progress of prebasic molt of primary feathers in female European starlings (mean 6 range). A timeline of different photoperiod exposures for each of two experiment groups is shown at the top and is aligned with the abscissa. Sample sizes refer to the number of females.

the hypothesis that an individual's having prior experience with photostimulation (hereafter photo-experience) elevates the rate or magnitude of reproductive development stimulated by photostimulation (hereafter photo-induced reproductive development). Like most bird species, wild-caught starlings will rarely lay eggs under photostimulation in small laboratory cages. However, laboratory photostimulation will drive many of the initial stages of reproductive development that must precede laying, were it to occur, and here we use these initial stages as a proxy for reproductive development in general. Specifically, we predicted that having photo-experience elevates the photo-induced increase in 1) body mass, associated in many species with preparation for laying; 2) secretion of GnRH; 3) secretion of LH; 4) development of the ovary, oviduct, and ovarian follicles; and 5) secretion of the yolk precursor vitellogenin. We assume in this study that changes in these measures in the laboratory reflect the beginnings of the suite of physiological processes that, in the wild, would eventually lead to egg laying.

MATERIALS AND METHODS

We conducted this study in accordance with the 1996 National Academy of Sciences *Guide for the Care and Use of Laboratory Animals* and with approval from the Johns Hopkins University Institutional Animal Care and Use Committee.

Premanipulation: Capture, Housing, and Initial Photosensitization

We captured European starlings in September 2001 on a farm near Baltimore, Maryland, and determined by their brown speckled plumage that they had all hatched that spring or summer [21]; we held them on a daily photoperiod of 8L:16D. Throughout the study we provided them with ad libitum access to food and water. In mid-November, we anesthetized (5 mg secobarbital injected i.m.) and sexed them by laparotomy.

Photo-Experience Manipulation

Twelve weeks after capture and onset of 8L:16D, we randomly paired 32 females in 16 sound-attenuation chambers, half on 8L:16D (naive group) spatially interspersed in one room with the other half on 16L:8D (experienced group; approximately 5 wk into this phase, one female in this group died and was excluded from analysis).

Beginning at Week 12, with the onset of this phase, and lasting through to Week 36 of the study, we periodically weighed individuals, scored prebasic primary feather molt using a previously described technique [22], and collected blood samples from wing veins into heparinized capillary tubes for assays of plasma vitellogenin and LH (see below). We stored blood on ice for a few hours prior to centrifugation for 9 min at 9000 rpm to separate plasma, which we stored at 2208C until assayed.

Eight weeks of 8L:16D is typically sufficient to ensure starlings are photosensitive [23], and 12 wk of 16L:8D is typically sufficient to drive starlings photorefractory [24]. However, one means of confirming photorefractoriness and thus to confirm that photocondition differed between the experienced and naive groups during the photo-experience phase is to quantify the progress of prebasic molt. The onset of prebasic molt presages and serves as an indicator of photorefractoriness because of the fact that both may be regulated by the same physiological mechanism [25, 26]. We determined that all experienced and no naive females initiated molt well in advance of the end of this photo-experience phase of the experiment (Fig. 1). This confirmed that, by the end of the photo-experience phase, all experienced and no naive individuals had been driven photorefractory.

Postmanipulation: Photosensitization Followed by Photostimulation of All Females

Twelve weeks after transfer to the chambers (and transfer to 16L:8D for the experienced group), we removed all females from the chambers and placed them in open wire cages together in one room on 8L:16D. After 8 wk, we changed the photoperiod to 16L:8D to simultaneously photostimulate naive individuals for the first time and experienced individuals for the second time in their lives. To summarize, after holding half the females (naive group) on 8L:16D for 32 wk and the other half (experienced group) on 8L:16D for 12 wk, 16L:8D for 12 wk, and then 8L:16D for 8 wk, we simultaneously photostimulated all of them. It is the period following Week 32 that is most relevant to our hypothesis (see *Introduction*), because during this time the naive group was experiencing photostimulation for the first time and the experienced group for the second time in their lives. In first-year female starlings, mean hypothalamic GnRH concentrations do not decline (i.e., females do not begin HPG regression) before 6 wk after transfer from 8L:16D to 18L:6D [27]. On 16L:8D, GnRH concentrations would decline even later. However, due to interindividual variation (from photo-experience or other factors) and to be sure that measurements occurred when photo-induced HPG capacity was still ascending, we anesthetized (6.5 mg secobarbital injected i.m.), killed, and collected the brains of all individuals for GnRH immunocytochemistry (see below) after 4 wk of photostimulation using procedures described previously [28]. Blind to the photo-experience of each individual, we also dissected and weighed ovaries and oviducts and estimated the diameter of the largest ovarian follicle.

Assays for Vitellogenin and LH

We assayed plasma vitellogenin indirectly using the zinc method developed for the domestic hen [29] and validated for passerines [16, 30]. Inter- and intraassay variation were 6% and 7%, respectively. Concentrations of vitellogenin-bound zinc depicted in the results are a reliable index for the concentrations of plasma vitellogenin (vitellogenin hereafter). We measured vitellogenin in the plasma of only one of the females from each photo-experience pairing (see above).

Using duplicate 20-ml aliquots of plasma, we assayed LH concentrations with a homologous chicken LH radioimmunoassay [31]. The antiserum was IRC M202 at a 1:5000 dilution. The sensitivity of the assay was 0.05 ng/ml, and 50% displacement was obtained with 2.4 ng/ml. All samples were assayed in one assay with 5.3% and 7.3% variation for a high- and a low-value pool, respectively.

GnRH Immunocytochemistry and Quantification

We performed immunocytochemistry for GnRH on 40-mm, sagittally cut brain sections, as previously described for the transcription factor ZENK [28], except we visualized the avidin-biotin horseradish-peroxidase complex in a 0.018% diaminobenzidine tetrachloride solution containing 0.01% H_2O_2. As part of another study, we initially labeled tissue for

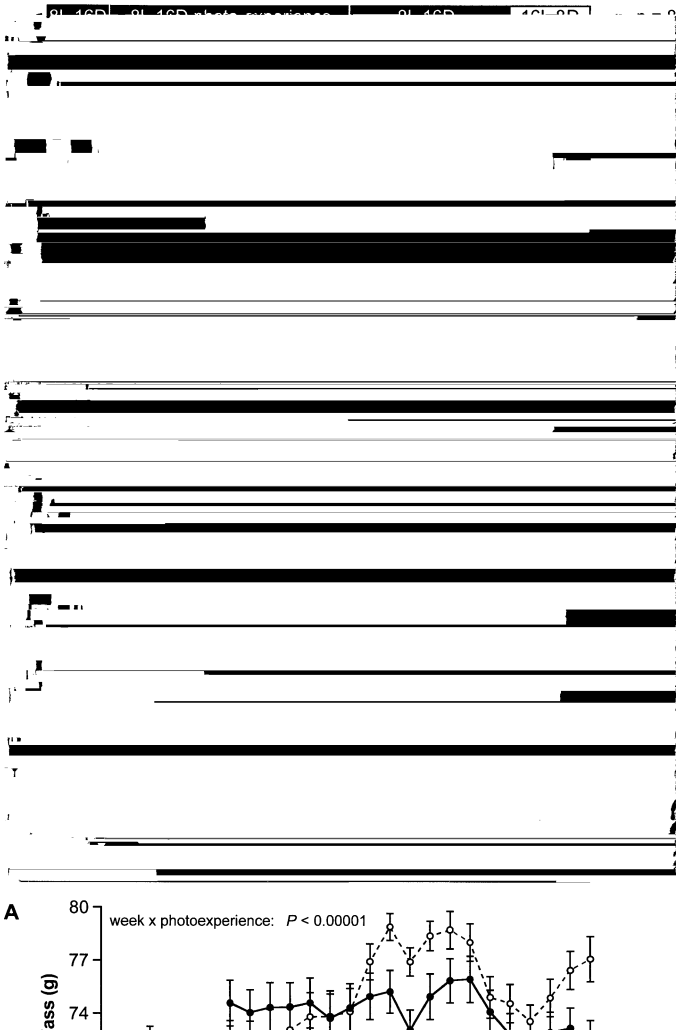
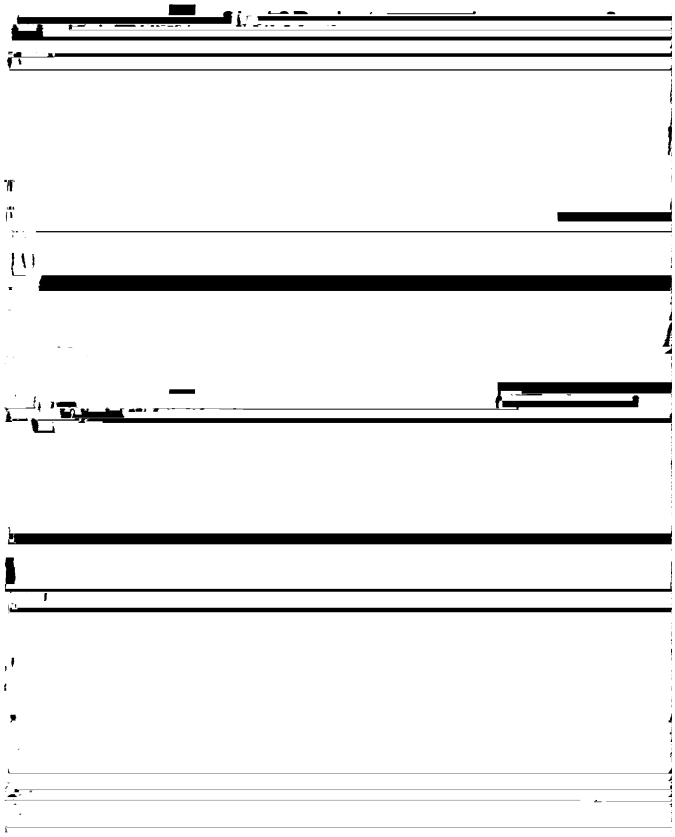


FIG. 2. Temporal change in body mass (**A**) and plasma concentrations of vitellogenic zinc (**B**) and LH (**C**) (mean 6 SEM) as a function of photoperiod and photo-experience in female European starlings. A timeline



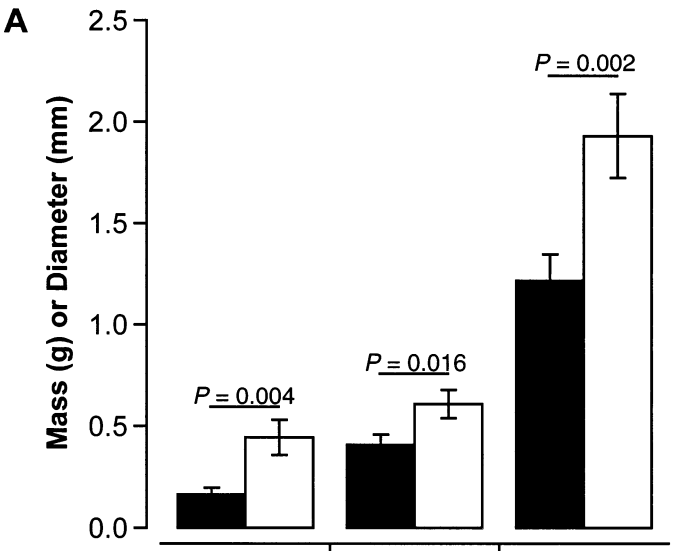


FIG. 3. Effect of prior photo-experience, (**A**) before and (**B**) after adjusting for body mass, on oviduct mass, ovary mass, and diameter of the largest ovarian follicle (mean 6 SEM) 4 wk following onset of photostimulation (Week 36) in female European starlings. Ovary mass is depicted at 10 times the estimated total. Sample sizes refer to the number of experiment units.

experience, and they were similar between groups at the start of the time period of primary interest, Week 32 (post hoc contrast, P 5 0.14; Fig. 2B). Photo-experience affected how plasma concentrations of vitellogenin changed over the remainder of the study (Week [32–36] 3 photo-experience effect, $F_{4,56}$ 5 3.13, P 5 0.021). By Week 34, although all individuals were under identical conditions, vitellogenin in the naive group rose to concentrations reliably greater than both those in the experienced group at that time (post hoc contrast, P 5 0.026) and those in the naive group at the onset of photostimulation (Week 32; post hoc LSD, P 5 0.0004). Thereafter, however, vitellogenin in the naive group declined while it increased in the experienced group. By Week 36, vitellogenin concentrations in the experienced group were higher (post hoc contrast, P 5 0.10), on average, than those in the naive group and reliably higher than they were at the onset of photostimulation (Week 32; post hoc LSD, P 5 0.0004). In contrast, the difference between Week-32 and -36 vitellogenin concentrations in the naive group was not particularly reliable (post hoc LSD, P 5 0.13).

Photo-experience affected how plasma concentrations of LH changed over the course of the study (Week [24–36] 3 photo-experience effect, $F_{6,84}$ 5 12.66, P , 0.00001). At the onset of the photo-experience phase of the study (Week 12), LH concentrations of the experienced group were nearly identical to those of the naive group (Fig. 2C). However, by 2 wk later, LH concentrations were substantially greater in the experienced group than in the naive group. By Week 18, LH concentrations in the experienced group had returned to the low levels of the naive group. Both groups remained similarly low through to the onset of the phase of primary interest at Week 32 (post hoc contrast, P . 0.2). Immediately following onset of 16L:8D at Week 32, LH concentrations in both groups increased, but the increase in the experienced group was substantially greater than that in the naive group, although all birds were under identical conditions. By 1 wk into the onset of this phase, LH concentrations in the experienced group were much higher than both the concentrations in the naive group at this time (post hoc contrast, P 5 0.001) and the concentrations in the experienced group at the onset of this phase (Week 32; post hoc LSD, P , 0.00001). The high concentrations in the experienced group then decreased to the moderately elevated levels of the naive group at Weeks 35 and 36, when levels in both groups were reliably elevated above levels at the onset of 16L:8D (Week 32; post hoc LSD, P , 0.037 each comparison).

Oviduct Mass, Ovary Mass, and Follicle Diameter

At the end of the study, 4 wk after onset of photostimulation in all individuals, oviduct mass (photo-experience effect, $F_{1,14}$ 5 11.52, P 5 0.004); ovary mass (photo-experience effect, $F_{1,14}$ 5 7.48, P 5 0.016); and follicle diameter (photo-experience effect, $F_{1,14}$ 5 14.68, P 5 0.002) were all reliably greater in the experienced group than in the naive group (Fig. 3a). However, some gonadal size differences between groups may have been the result of the greater body mass of experienced individuals at the time of sacrifice (see Fig. 2a). When Week-36 body mass was included in the model as a covariate, the effects of photo-experience on oviduct (photo-experience effect, $F_{1,13}$ 5 3.37, P 5 0.089) and ovary mass (photo-experience effect, $F_{1,13}$ 5 2.39, P 5 0.15) became somewhat less reliable (Fig. 3b). The effect of photo-experience on follicle diameter (photo-experience effect, $F_{1,13}$ 5 6.34, P 5 0.026) remained quite reliable when we controlled for body mass, indicating a high likelihood that the larger follicles of experienced females were, at least in part, independent of their larger body mass.

GnRH-ir Cell Count, Cell Diameter, and Fiber Count

At the end of the study, 4 wk after onset of photostimulation in all individuals, the GnRH-ir cell count was

greater in the naive than in the experienced group (photo-

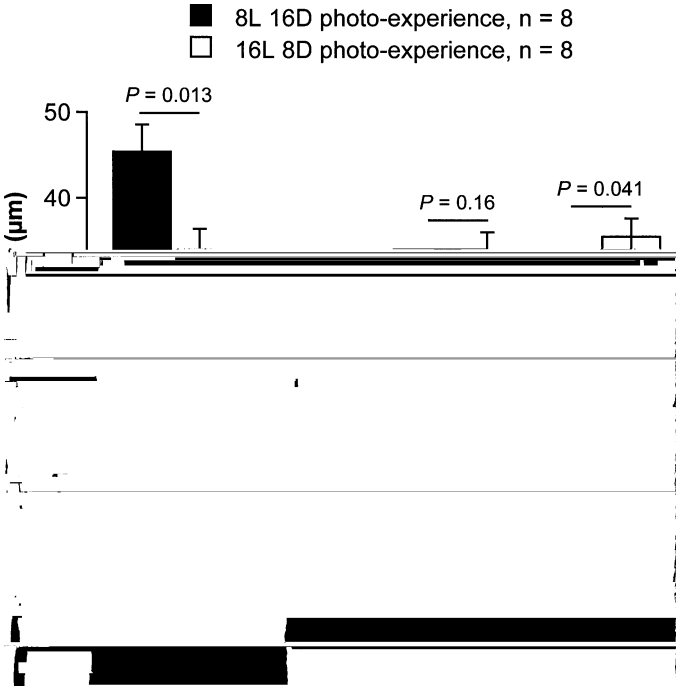


FIG. 4. Effect of prior photo-experience on number of septo-preoptic cell bodies immunoreactive for GnRH, mean GnRH-ir cell-body diameter, and number of septo preoptic GnRH-ir fibers before and after adjusting for the number of cell bodies 4 wk following onset of photostimulation (Week 36) in female European starlings (mean 6 SEM). The number of GnRH-ir neurons are depicted at 10^{21} of the estimated total. Sample sizes refer to the number of experiment units.

do not sustain such peak levels even for as long as a week. Therefore, one might hypothesize that perhaps the major difference between first- and second-year photostimulated females is not the magnitude of the LH surge but rather its timing, with second-year females reaching that peak approximately 1 wk prior to first-year females. Alternatively, high LH concentrations in experienced females on Week 13 would indicate that the duration of the LH surge is attenuated with photo-experience, perhaps as a result of a more effective feedback system.

We would expect the elevated LH concentrations of experienced, photostimulated females to result in greater or earlier stimulation of the gonad compared with naive, photostimulated females. Indeed, experienced females had a larger ovary and oviduct, but this effect may have been the result of their larger body mass. However, follicle diameter was larger in experienced than in naive females, irrespective of body mass. This alone is perhaps our most convincing evidence that experience with photostimulation elevates the rate or magnitude of photo-induced reproductive development in the starling, because unlike the relatively transient changes in LH, vitellogenin, and GnRH concentrations, follicle diameter reflects the integration of numerous factors over a longer period of time. Consistent with these findings, recent photoperiodic experience can influence subsequent, photo-induced gonad and body growth in young mammals [45–47], suggesting that the ability to somehow ''encode'' photoperiodic history applies to multiple vertebrate taxa. It should be noted for our study, however, that oviduct mass, ovary mass, and follicle diameter were all much lower than values in females nearing lay [15], regardless of photo-experience. But the values we observed are typical for photostimulated, laboratory-housed, wild-caught female starlings [48]. We assume that differences between experienced and naive females in this experiment reflect those that would occur during the earliest stages of photo-induced reproductive development, differences which would eventually lead to an older, free-living female laying sooner and more eggs than a younger one.

Having photo-experience is not required for an initial, photo-induced elevation in vitellogenin, as vitellogenin in both groups initially increased with photostimulation at Week 32. The fact that no such increase occurred for experienced females exposed to photostimulation the first time (Week 14) suggests an age-dependent process underlying a female's ability to respond to long days with vitellogenin secretion, although we may have missed an increase between Weeks 14 and 18. Where photo-experience appears to play a role is in the longer term elevation of vitellogenin, whereby experienced females have a more robust prolonged response than naive females. We offer this hypothetical explanation. Extended short-day exposure elevates liver stores but not synthesis of vitellogenin, possibly because short days inhibit secretion. Due to an accumulation of stores in naive females, photo-induced secretion is elevated initially but cannot be sustained with comparable synthesis. Females with normal short-day exposure respond more slowly because of low stores but, with photo-experience, can sustain the response because of elevated synthesis. Some evidence in birds for a so-called ''memory effect'' of the vitellogenin II gene provides support for this hypothesis [49]. Specifically, secondary estradiol exposure elevates mRNA concentrations over initial exposure. This would seemingly facilitate longer term high secretion rates. However, some caution is merited here as well. First, the memory effect shown previously occurred over a period of several hours, but was not tested over several weeks. Second, regardless of photo-experience or photoperiodic condition, vitellogenin concentrations in our study were much lower than those of a female starling undergoing rapid yolk deposition in preparation for ovulation [50, 51]. Still, as for gonad size (see above), we assume these low, rising levels reflect the initial changes that subsequently lead to egg laying in free-living females.

McNaughton et al. [52] found in starlings that repeated exposure to GnRH primes pituitary LH secretion, resulting in increasing concentrations of secreted LH with each additional exposure to GnRH. They also found that, in terms of LH secretion, the pituitary was substantially less responsive to GnRH injection in photorefractory juvenile starlings than in photorefractory adults, which would have had prior experience with high GnRH exposure. One interpretation of their findings is that GnRH upregulates its own receptors on the pituitary, a process that occurs in mammals [53]. These studies suggests a mechanism for the results presented here and indeed for the age-related increase in re-

fiber should increase with GnRH sequestration, with increasing secretion, fiber relative to cell-body content of GnRH should also increase as the result of the one-way movement of GnRH molecules from cell bodies to cell fibers to the extracellular portal vascular system. In other words, with increasing secretion rates, we would expect relatively greater intracellular distribution of GnRH away from cell bodies and toward fibers and the portal vasculature. This is indeed what we found, and together with our results on LH concentrations, vitellogenin concentrations, and follicle size, this suggests that females with photo-experience have higher photo-induced GnRH secretion rates than females without such experience. However, confirmation of these findings awaits more direct measures of GnRH secretion.

We have found that photo-experience elevates the rate or magnitude of some of the initial stages of photo-induced reproductive development in a temperate zone, female songbird. We suggest that in free-living females, the elevation of these initial stages would give rise to laying earlier and more eggs and would explain, in part, why reproductive performance is often higher in older than in younger birds. Certainly other experiences, such as feeding young [55], may also enhance reproductive performance.

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