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Endocrine Changes Associated with Spawning Behavior and Social Stimuli in a Wild Population of Rainbow Trout (*Salmo gairdneri*)

II. Females

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Rainbow trout (*Salmo gairdneri*) were collected from a natural spawning population at Pennask Lake, B.C. Blood samples taken from female trout at different stages of spawning were assayed by radioimmunoassay for gonadotropin (GtH), estradiol-17 β (E₂), androgens, including testosterone (T), and 17 α -hydroxy-20 β -dihydroprogesterone (17,20-P). Plasma levels of androgen and estradiol were highest in females sampled shortly before ovulation ("green" females) and declined in ovulated and sexually active females, reaching lowest levels in postspawning fish. Concentrations of 17,20-P rose markedly in ovulated females allowed to dig nests and interact with sexually active males. Plasma GtH levels were similar in green unovulated females and ovulated fish prevented from spawning, but showed a marked increase in actively nest building ovulated fish. The results demonstrate that social stimuli affect plasma levels of 17,20-P and perhaps GtH. The functional significance of the endocrine responses to social factors is not clear, but it is suggested that increased hormone levels may contribute to an acceleration or synchronization of breeding, or be responsible for causing and maintaining more vigorous sexual activity. © 1986 Academic Press, Inc.

There has been considerable progress in recent years in describing the endocrine changes associated with reproduction in teleost fish (recent review by Fostier *et al.*, 1983). These investigations provide us with a clear overview of the major annual and seasonal endocrine events associated with reproduction, but they provide almost no information regarding the role of endocrine factors in the regulation of prespawning and spawning behavior (Liley and Stacey, 1983).

In addition to the lack of information regarding a behavioral role for any of the gonadal steroids or other hormones, little is known of the extent to which acute changes in endocrine factors are governed by stimuli provided by social partners or competitors, or by features of the environment such as the availability of suitable spawning substrate. Studies of both mammals and birds have demonstrated the

importance of the two-way relationship between the social environment and the endocrine system in the coordination of reproductive activities (Silver and Cooper, 1983; McClintock, 1981). A number of studies, reviewed by Liley (1980) and Lam (1983), point to the role of chemical and behavioral signals in accelerating or synchronizing breeding in fish. Presumably, effects of this nature are mediated by the endocrine system. Direct evidence of behaviorally induced endocrine changes has been provided by Kyle *et al.* (1982, 1985) who found a rapid increase in plasma gonadotropin in male goldfish exposed to a spawning pair. Similarly, Liley *et al.* (1985) demonstrated marked increases in gonadotropin (GtH) and 17 α -hydroxy-20 β -dihydroprogesterone (17,20-P) in male rainbow trout exposed to nest building females.

A major reason for the lack of understanding of the behavioral role of gonadal

and other hormones, and the extent of acute endocrine responses to environmental stimuli, is that most studies have concerned captive fish not allowed to participate in a normal spawning process. This is particularly true of investigations involving domesticated strains of rainbow trout, many generations removed from their wild progenitors.

In the present study blood samples were taken from females of a wild population of rainbow trout at different stages of the natural spawning cycle. The objectives of this approach were: (a) to compare the plasma hormone profiles of wild fish with those obtained in hatchery stocks, (b) to provide information on acute, short-term changes in endocrine condition associated with particular events during spawning, perhaps providing information on possible causal relationships between endocrine factors and behavior, and (c) to evaluate the influence of certain social and physical stimuli on the endocrine condition of the fish.

MATERIALS AND METHODS

The trout stock, spawning behavior, methods of collection and behavioral observation, and analysis of results (significance set at $\alpha = 0.05$) are as described in Liley *et al.* (1986).

Radioimmunoassay procedures were also similar except that in the first experiment (1982) "androgens" in female plasma were measured with a nonspecific antibody cross-reacting with testosterone (100%), 11-ketotestosterone (61%), 5 α -dihydrotestosterone (84%), androsterone (18%).

In the second experiment (1983) a more specific antibody against testosterone was used. Cross-reactivities when conducted on females were: testosterone (100%), 5 α -dihydrotestosterone (41%), 11-ketotestosterone (31%), androstenedione (14%), 5 α -androstan-3 α ,17 β -diol (6%); 5 α -androstan-3 β ,17 β diol (2%), adrenosterone (0.2%); androsterone (0.2%); dehydroepiandrosterone (0.1%).

PLASMA HORMONES IN FISH SAMPLED AT THE SPAWNING SITE, 1982

Blood samples were taken from the following groups:

(a) "Green" unovulated females. Fish

taken directly from the trap before "stripping" began; June 15; $n = 12$; standard length (SL) = 30.7 cm \pm 0.59 SE; weight 372.5 g \pm 21.1 SE. These females had not ovulated: the abdomen was firm and eggs could not be obtained even under strong pressure.

(b) *Ovulated females*. Fish taken from hatchery personnel immediately after being stripped of eggs; June 23, $n = 10$. Just prior to stripping, these females had soft abdomens and released eggs freely as a result of gentle pressure.

(c) *Postspawning females*. Fish taken from above the trap after they had completed a natural spawning; June 28, $n = 10$. Females in this group were thin, had lost their spawning coloration and, in a few cases, yielded a small number of eggs under strong pressure.

(d) *Nest building females*. Fish allowed to establish a nest and complete one spawning, $n = 5$, June 25–30. These females were removed and sampled while actively nest building and probing.

(e) *Inactive ovulated females*. Fish in this group had been tested for ovulation and placed in spawning channels to become part of the group of nestbuilding females. Heavy rainfall and snow caused a drop in temperature from 12 to 6° and a rise in water levels. These females left the gravel and became inactive and were sampled on July 5, four days after the change in conditions, $n = 8$; SL = 32.5 cm \pm 2.8 SE.

Results

Gonadotropin. Although the analysis of variance indicates significant differences among the groups, none of the paired comparisons is significant at $P < 0.05$ (Fig. 1). GtH levels in nest building females and "inactive" females tended to be higher than the other three groups.

Estradiol was undetectable in any of the nest building females; differences among the other groups were not significant.

Androgen levels were highest in the

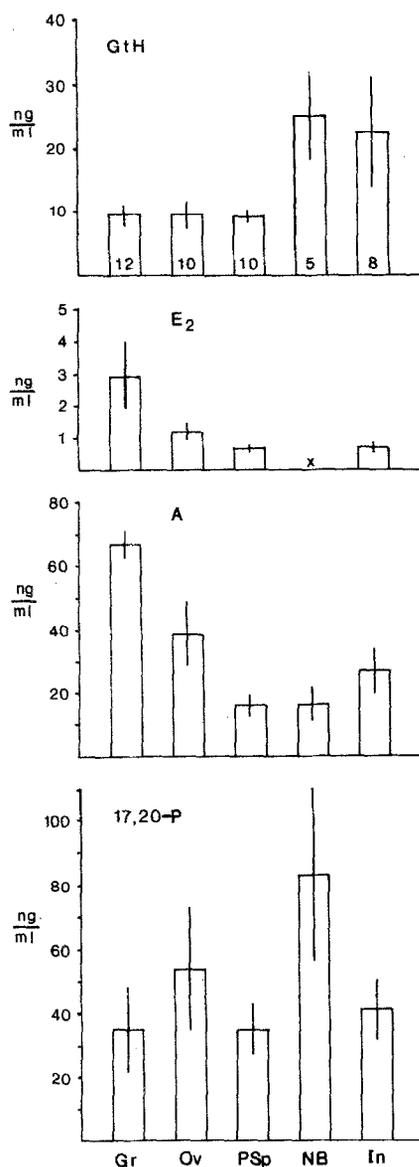


FIG. 1. Plasma levels (mean \pm SE) of gonadotropin (GtH), estradiol-17 β (E₂), androgen (A), and 17 α -hydroxy-20 β -dihydroprogesterone (17,20-P) in female rainbow trout at different stages of the spawning cycle, 1982: Gr = "green" unovulated; Ov = ovulated; PSp = postspawning; NB = nest building female; In = ovulated but inactive fish. Sample sizes shown at base of each column of the upper histogram. X = undetectable.

"green," unovulated females: all other groups had significantly lower levels than

green females but did not differ significantly among themselves.

Progesterin (17,20-P) levels did not differ significantly among the groups. As in the case of the measures of GtH the highest plasma hormone levels were found in nest building females.

PLASMA HORMONES IN FISH SAMPLED IN THE LABORATORY, 1983

All females were in an unovulated condition when they were collected from the fish trap. Fish were established in the following experimental groups in the laboratory.

Group A. Females found to have ovulated within 2 days of collection were placed in channels and allowed to establish a nest and interact with courting males before the 1st blood sample was taken (A1), $n = 14$; SL = 33.1 cm \pm 0.39 SE; wt 356 g \pm 12.2 SE. After sampling, several of the females were removed from the spawning channel and placed in a tank without gravel with several other females but no males. Under these conditions all reproductive activity came to a halt. After being separated from males for 3–5 (mean 4.5) days the females were bled a second time (Sample A2, $n = 6$). The remaining fish in this group were allowed to continue reproductive activity and then sampled a second time—in two cases after actual spawning (A3, $n = 5$).

Group B. This group consisted of females in green, unovulated condition placed with males in spawning channels 1–2 days after arrival from the field: $n = 17$; SL = 32.1 cm \pm 0.36 SE; weight 328 g \pm 14.4 SE. All were sampled on the third day (B1) before any reproductive activity commenced. Eleven females were resampled 1–10 days ($\bar{x} = 3.8$) later, after they had begun nest building (B2).

Group C. These were green females held in isolation from males in a tank without gravel, $n = 12$; SL = 32.1 cm \pm 0.58 SE;

weight $320 \text{ g} \pm 13.15 \text{ SE}$. They were checked periodically for ovulation. The first blood sample was taken 3–5 days ($\bar{x} = 3.8$) after ovulation was recorded (C1). After taking the first sample the females were placed with males in a spawning channel and allowed to commence spawning activity and then resampled (C2, $n = 7$).

Group D. This group consisted of post-spawning females which had become sexually inactive after spawning or being stripped of eggs. In some cases the female had been allowed to complete normal spawning before sampling, $n = 5$. Others were ovulated and had begun nest building: they were stripped of eggs and returned to spawning channels to be sampled only when it was established that no further nest building activity had occurred, $n = 8$. All females in D: SL = $33.9 \text{ cm} \pm 0.6 \text{ SE}$; weight $372 \text{ g} \pm 22 \text{ SE}$.

Results

Most females of group A began digging a nest and were actively courted by males within 5 days of transport to the lab ($\bar{x} = 4.8$ days, range 2–9). Blood samples were taken (A1) as soon as a nest was well established. All females performed frequent digging and probing and were actively courted by males (Table 1). Green, unovulated females of group B showed almost no nest building activity and attracted little courtship attention from males (Table 1). The first sample was taken while the female

was still inactive. As the females began digging and attracted male attention a second sample (B2) was taken 1–10 days ($\bar{x} = 3.8$) after the first. Both male and female prespawning activity increased dramatically (Table 1). All persistently nest building females were found to have ovulated ($n = 11$): two B females were ovulated but did not dig nests; three remained unovulated and sexually inactive when observations were ended more than 9 days after the first sample was taken. Females of group C, which ovulated while being held in bare tanks without males, made no attempt to nest or deposit eggs. After taking the first blood sample (C1) the females were placed in a spawning channel. Nesting began, in some cases within 2 hr: the second sample (C2) was taken from 3 hr to 7 days ($\bar{x} = 2$ days) after the first, once nesting was well established.

The first samples taken from actively digging females in group A had the highest GtH levels of any group of fish held in the laboratory (Fig. 2), significantly higher than in first samples taken from green females (B1) and females becoming ovulated while isolated from males (C1), but not significantly greater than postspawning females (D). The differences in GtH levels between the first sample (A1) and the second sample from females isolated from males for 3–5 days (A2), or in females allowed to continue spawning activity for up to 4 days before the second sample was taken (A3) were not significant. However, the decrease in GtH between first and combined second samples, A1 compared with A2 and A3 combined, was significant.

Unovulated females placed in spawning channels with males and sampled while green (B1) had significantly lower GtH levels than females already ovulated and nest building (A1) shortly after transfer from the field. There was no change in GtH levels as these females ovulated and became active (B2).

In females isolated from males and

TABLE 1
MEAN FREQUENCIES OF MALE COURTSHIP AND FEMALE NESTING ACTIVITY IN 20 MIN PRIOR TO TAKING BLOOD SAMPLE

Female group	n	Bouts of quiver by male	Bouts of female	
			Dig	Probe
A1 (ovulated)	11	18.6 ± 3.2	21.3 ± 9.9	16.8 ± 3.6
B1 (unovulated)	17	1.9 ± 0.7	0.12 ± 0.08	0
B2 (ovulated)	11	13.4 ± 1.3	19.9 ± 3.3	41.0 ± 5.9

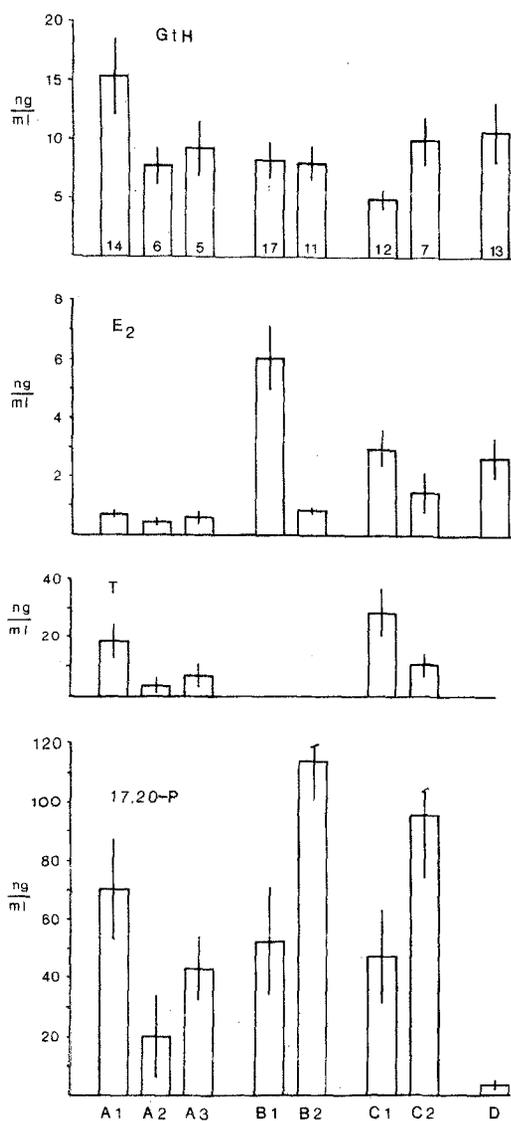


FIG. 2. Plasma levels (mean \pm SE) of gonadotropin (GtH), estradiol-17 β (E₂), testosterone (T), and 17 α -hydroxy-20 β -dihydroprogesterone (17,20-P) in female rainbow trout under different social and environmental conditions in the laboratory: A1 = ovulated, nest building females, A2 = same females placed in isolation, or allowed to continue courtship = A3; B1 = "green" unovulated and sexually inactive females, B2 = same females after ovulation and start of nest building; C1 = females ovulated in isolation from male and gravel, C2 = same females placed with males and allowed to nest build; D = inactive post-spawning females. Sample size shown at base of each column of the upper histogram.

gravel, while still green, and allowed to ovulate, GtH levels (after ovulation) (C1) were found to be significantly lower than in females in A1, but not different from the B fish. Transfer to a spawning channel (C2) resulted in an increase in GtH ($P < 0.031$, 1-tailed test). The GtH levels of post-spawning fish (D) are similar to those of groups A2 and 3, B1 and 2, and C2, but significantly greater than C1.

Estradiol (E₂) levels were low in all A samples (Fig. 2). Plasma E₂ levels were highest in green females (B1) and showed a highly significant decline as those females ovulated and became sexually active. In the ovulated but isolated females of group C1 levels of E₂ were significantly higher than in A1 but did not differ from B1. Sexually active females of the C group (C2) and the postspawning females of group D had E₂ levels similar to those of B1 and C1 fish.

Testosterone (T) was measured in two groups A and C (Fig. 2). In both, the levels of T were considerably higher than E₂. There was no significant difference between ovulated active females (A1) and ovulated isolated females (C1). There appeared to be a decline in T in both groups but in neither case was the difference significant.

Progesterin (17,20-P) levels were high in actively nest building ovulated fish (A1) and declined markedly in the same fish placed in isolation (A2) ($P < 0.05$, 1-tailed test) (Fig. 2). Fish allowed to continue nest building in the presence of a male (A3) showed a less marked decline in 17,20-P which was not significant. The difference between A2 and A3 was significant ($P < 0.05$, 1-tailed test, direction of difference predicted), however, it should be noted that the second sample in A3 was taken after an interval of a maximum of 2 days, whereas A2 was taken 3–5 days after A1.

Plasma levels of 17,20-P in green females (B1) were similar to those of the ovulated females A1 and C1. The onset of ovulation and spawning activity was accompanied by

a marked, significant increase in 17,20-P, compare B1 and B2. Similarly in group C, placing ovulated females into spawning channels with males was accompanied by an increase in progesterin ($P < 0.04$, 1-tailed test). Ovulated nest building females of group B2 had significantly higher 17,20-P levels than ovulated females maintained in isolation before the first blood sample was taken (C1). After placing the ovulated females in spawning channels 17,20-P increased (C2) to a level similar to that of B2. In postspawning fish 17,20-P fell to concentrations significantly lower than those of any other group.

The occurrence of spawning cannot be correlated with any particular endocrine condition. Seven females were known to have spawned less than 2 hr prior to taking blood samples; another 5 had spawned within the preceding 24 hr. Plasma hormone levels of these fish were well within the range of active but nonspawning individuals in groups A1, B2, or C2 (data not shown).

DISCUSSION

Pennask Lake fish spawn in June and early July. In hatchery populations examined in previous studies female rainbow trout are in spawning condition for limited periods from November to March (e.g., Scott and Sumpter, 1983). Presumably these differences in spawning season reflect differences in the original stocks, and are also to some extent the result of selection under domestication. In spite of striking differences in the time of spawning the overall pattern of changes in hormone levels observed in this study are in agreement with those described elsewhere for rainbow trout (Scott *et al.*, 1980, 1983; van Bohemen and Lambert, 1981; Fostier *et al.*, 1978, 1981b; Schulz, 1984). All studies reveal a decline from peak levels of estrogen (>50 ng/ml) several weeks before ovulation to less than 10 ng/ml immediately before or just after ovulation. In this inves-

tigation fish were evidently in the last phase of this decline; estradiol levels were highest in green females (3 ng/ml in 1982) several days before ovulation and declined further in ovulated fish to less than 2 ng/ml. In the B group in 1983 there was a highly significant decline over a period of 4 days as green females became ovulated and began nestbuilding. Estrogen levels remained low in spawning and postspawning fish.

Plasma testosterone has been measured at levels in excess of 200 ng/ml before ovulation in rainbow trout: in some investigations peak levels of T occurred 4–6 weeks prior to ovulation (Scott *et al.*, 1980, 1983), in others a peak occurred about 1 week before ovulation (Fostier and Jalabert, 1982; Scott and Baynes, 1982). Testosterone decreased rapidly throughout the weeks before ovulation and continued to decline during the period of ovulation, though concentrations remained well above those recorded for estradiol. In this study plasma levels of androgens were highest in green fish sampled in 1982 (mean 66 ng/ml), and declined in ovulated and sexually active females, reaching the lowest levels in postspawning fish.

In hatchery trout the levels of progesterin 17,20-P, increase dramatically from being almost undetectable in prespawning females to mean values in excess of 300 ng/ml at ovulation (Fostier *et al.*, 1981b; Scott *et al.*, 1983). Similar dramatic increases have been recorded in Pacific and Atlantic salmon (Ueda *et al.*, 1984; Wright and Hunt, 1982; Young *et al.*, 1983). Concentrations of 17,20-P measured in this study were considerably lower (maximum mean = 113 ng/ml). The assay used here was the same as that used by Fostier *et al.* (1981a), suggesting that there may be real differences in the plasma levels of 17,20-P in Pennask fish and the hatchery stock used by Fostier *et al.*

After spawning, levels of 17,20-P decline slowly in hatchery fish (Fostier *et al.*,

1981b; Scott *et al.*, 1983). There is a suggestion that postovulatory changes in 17,20-P levels may be governed by the incidence of spawning or stripping procedures. Young *et al.* (1983) noted an increase in the capacity of postovulatory follicles to secrete 17,20-P. They propose that the maintenance of high levels of 17,20-P after ovulation may depend upon the retention of eggs. The evidence provided by this study is conflicting: 17,20-P concentration fell to very low levels in inactive postspawning fish in the 1983 experiments, whereas in the 1982 collections postspawning females had levels similar to those of the other groups including the ovulated but sexually inactive females which *retained the full complement of eggs*.

The 1983 data provide evidence of an effect of social stimuli on plasma levels of 17,20-P. Levels of the progestin showed a marked decline in nest building females removed after the first sample and isolated from males and spawning substrate (A2). Although 17,20-P also declined in females allowed to continue spawning, the decrease was less marked and not significant. It should be noted, however, that in the former case the second sample was taken 3–5 days after the first, whereas in the latter group the interval was in most cases only one day. The low level of 17,20-P in postspawning fish suggests that this steroid reaches a peak at the time of ovulation and declines thereafter. The effect of social stimulation and perhaps the retention of eggs (see above) may be to delay, to a limited extent, this decline.

The striking increase in plasma 17,20-P in group B females sampled first in green condition and then after ovulation could be in part a response to social stimulation as well as the increase in 17,20-P accompanying and perhaps responsible for ovulation. The strongest evidence for an effect of social stimuli comes from those females held in isolation and sampled after ovulation while still in isolation (C1). Those fe-

males had lower levels of 17,20-P than ovulated females exposed to male courtship and allowed to build nests (B2), and not significantly different from the green females in B1. Transfer of the previously isolated ovulated females to spawning channels resulted in a doubling of the mean 17,20-P concentrations (C2).

These data strongly suggest that, as demonstrated in previous studies, there is a marked increase in plasma levels of 17,20-P at the time of ovulation. But, in addition, stimuli associated with the presence of a male and spawning substrate maintain and perhaps stimulate a further increase in plasma 17,20-P. In the absence of such stimuli 17,20-P levels decline.

Gonadotropin levels remain relatively low throughout much of the prespawning period in rainbow trout but rise sharply just before ovulation (Fostier *et al.*, 1978) and may continue to rise, reaching a peak 20 days after ovulation (Fostier *et al.*, 1981a; Scott *et al.*, 1983). A similar increase in GtH associated with ovulation and spawning has been noted in a variety of salmonid species (Breton *et al.*, 1983; Crim *et al.*, 1975; Fostier *et al.*, 1978; Young *et al.*, 1983; Ueda *et al.*, 1984). The samples taken in this study correspond to the final stages in the reproductive cycle. The highest levels of GtH recorded in the 1983 samples were in the actively nestbuilding ovulated fish where they were significantly higher than in green females or females which had spontaneously ovulated in isolation.

There is no clear evidence of an effect of social stimulation on GtH: levels showed a similar decline in both of the second samples of the A group, that is, those in isolation and those allowed to continue spawning. Surprisingly, there was no increase in paired green females as they ovulated and commenced spawning activity. There was an increase in GtH in previously isolated females after pairing in a channel.

A number of authors have commented

upon the fact that in contrast to female cyprinids (Scott *et al.*, 1984) gonadotropin levels in female rainbow trout remain high or even increase after ovulation. Scott *et al.* (1983) suggest that this rise in GtH for 3 weeks after ovulation may reflect a reduction in steroid negative feedback. These authors were unable to confirm Jalabert and Breton's (1980) finding that postovulatory GtH levels were higher in females retaining eggs than in stripped fish. Jalabert and Breton (1980) proposed that the high levels of GtH may be involved in maintaining the viability of retained ovulated eggs which remain fertile for several days after ovulation (Escaffre *et al.*, 1977; Bry, 1981; Craik and Harvey, 1984). In this study there was no evidence of any increase in GtH in post-spawning fish in either year. Ovulated fish, sexually inactive for several days, showed levels of GtH similar to prespawning groups.

Because of the established tropic action of GtH upon secretion of 17,20-P (Fostier *et al.*, 1981a; Scott *et al.*, 1983; Young *et al.*, 1983) it might be expected that changes in 17,20-P would reflect changes in GtH. But in the group with the most striking change in 17,20-P concentration, green females that became ovulated and began spawning activity, the rise in this steroid was not accompanied by an increase in GtH. It is possible that a preovulatory rise in GtH responsible for the increase in 17,20-P had already occurred by the time the green females were sampled. Scott *et al.* (1984) propose that in white suckers, *Catostomus commersoni*, the preovulatory increase in GtH requires several days to elevate progesterin levels. However, the presence of relatively low levels of GtH in green females, compared with the females already ovulated the day after collection, does not support that explanation. Interestingly, males paired with many of the same females showed a similar dissociation of 17,20-P and GtH changes. In that case plasma levels of GtH were high in males

paired with green females and 17,20-P rose only after the females had ovulated (Liley *et al.*, 1986). Furthermore, there is evidence that in males changes in 17,20-P levels may occur within hours of exposure to social stimuli.

The functional significance of these endocrine responses to stimuli from the spawning situation is not clear. Although ovulation occurs spontaneously in females isolated from males, the increased hormone levels resulting from social stimulation may contribute to an acceleration or synchronization of breeding, or be responsible for causing and maintaining more vigorous sexual activity. Ovulated females will commence nestbuilding in the absence of a courting male, but casual observation suggests that such nestbuilding is weak and less persistent than in females paired with males, indicating that male signals are important in maintaining vigorous nesting activity either directly or through the mediation of the endocrine system. The possibility that a progestin or GtH stimulate female reproductive activity directly should certainly be examined.

Evidence that social signals play a role in the acceleration and synchronization of ovulation and subsequent spawning has been obtained in the danio *Brachydanio rerio* (Chen and Martinich, 1974) and the angel fish *Pterophyllum scalare* (Chien, 1973). In both species a pheromone released by the male is believed to accelerate gametogenesis and stimulate ovulation in conspecific females. Sound and visual signals have been implicated in hastening vitellogenesis and ovulation in tilapia *Sarotherodon mossambicus* (Marshall, 1972; Silverman, 1978). Yamazaki (1965) suggested that the presence of male goldfish stimulates ovulation in females. Stacey *et al.* (1979) were unable to confirm this, but did demonstrate that the presence of a spawning substrate, aquatic vegetation, plays a role in the induction of ovulation.

No attempt was made to identify the ef-

fective components in the spawning situation. The onset of weak nest building in the absence of males indicates that for full reproductive activity both substrate and male are important. It is likely that visual, tactile, and chemical signals are all important. Newcombe and Hartman (1973) found that female rainbow trout were strongly attracted to water that had held ripe males or to water taken downstream of spawning trout. Other sensory cues have not been examined systematically.

A number of authors have speculated that gonadal and pituitary hormones may be involved in the regulation of sexual behavior in female salmonids. Scott *et al.* (1983) suggest that the high level of testosterone in females may not be simply a "by-product" resulting from changes in biosynthetic pathways, but that testosterone may act as a hormone responsible for the maintenance of sexual behavior and gonadotropin production during spawning. Crim *et al.* (1975) suggest that the high levels of GtH present in spawning fish are in some way involved in regulating behavior. However, at the present time there is no clear evidence that estradiol, testosterone, or gonadotropin play a direct causal role in reproductive behavior. At the time of spawning plasma estradiol and testosterone are rapidly declining from previous high levels, suggesting that either, or both, may play priming roles rather than being directly responsible for the onset of spawning activity. [A major function of estradiol is almost certainly its role in the stimulation and maintenance of vitellogenesis (van Bohemen *et al.*, 1982; Fostier *et al.*, 1983).] Either hormone could play a role in the prespawning migration from lake to river, and the relatively high levels of testosterone at spawning could reflect an involvement in the high level of aggression found in female trout defending the redd against neighboring females.

The dramatic increase in plasma levels of 17,20-P associated with ovulation and the

onset of spawning suggests the possibility that this hormone may be involved in the regulation of reproductive behavior as well as serving as the follicular mediator of GtH-induced maturation (Goetz, 1983; Nagahama *et al.*, 1983). This effect may be produced directly, or indirectly through an effect on the synthesis of prostaglandin (Young *et al.*, 1983). Prostaglandins increase at the time of ovulation and may be the natural mediators of oocyte expulsion (Goetz, 1983). Prostaglandins have also been implicated in the control of spawning behavior in females of a number of fish species (Liley and Stacey, 1983). Indirect evidence that prostaglandins regulate sexual behavior in female trout is provided by the finding that indomethacin, an inhibitor of prostaglandin synthesis, suppresses nest building activity (Liley, in preparation). However, attempts to restore sexual behavior by treatment with the prostaglandin $\text{PGF}_2\alpha$ were unsuccessful.

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