

Environmental Predictability and Control of Gonadal Cycles in Birds

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ABSTRACT In most vertebrates, information from the external environment is used to regulate secretion of gonadotropins and thus time gonadal maturation in anticipation of the breeding season. These environmental factors provide “predictive” information in both the long term (initial predictive) and short term (supplementary), are integrated by the central nervous system, and are then transduced into neuroendocrine and endocrine control components. We apply the constancy/contingency model of predictability to breeding data from several avian species to derive a potential unifying hypothesis to explain how these environmental factors are integrated to regulate gonadal maturation. Predictability (**Pr**) is a function of varying degrees of constancy (**C**, the habitat is predictable because it is always the same) or contingency (**M**, the habitat is predictable in the degree of change from season to season). Thus, although variations in **Pr** provide useful information for timing gonadal maturation and regression, changes in the contributions of **C** and **M** to **Pr** (i.e., the ratio, **M/C**) provide even more useful information. It is proposed that the degree to which individuals integrate initial predictive and supplementary information to regulate secretion of gonadotropins, and thus time gonadal maturation and onset of breeding, is a function of the ratio of **M** to **C** for any given **Pr** value. When **Pr** is not significant (i.e., the environment is unpredictable), then only supplementary factors may be useful for timing breeding. Hypotheses generated by this approach are easily testable. Furthermore, this method could be applied to all vertebrates, and perhaps other organisms, and may provide a unifying framework to investigate the mechanisms by which proximate environmental factors regulate reproductive function in general.

With few exceptions, vertebrates have discrete periods of breeding and non-breeding that are accompanied by gonadal maturation and regression. In birds, systems controlling cycles of gonadal function that accompany periodic breeding have received considerable attention (e.g., Farner, '70, '75, '85; Farner and Follett, '79; Farner and Gwinner, '80; Murton and Westwood, '77; Gwinner, '87; Berthold, '88; Follett, '84; Wingfield and Farner, '80 for representative reviews). Fluctuations in reproductive status are frequently annual and include changes in gametogenic as well as endocrine components. The latter, particularly production of sex steroids, is important not only for maturation of gametes (Brown and Follett, '75) but also for development of some secondary sex characters (e.g., Witschi, '61) and reproductive behavior (see Harding, '81; Balthazart, '83; Wingfield and Moore, '87; Wingfield et al., '87 for reviews). The breeding period is terminated when the gonad regresses to a non-functional state.

The timing and duration of breeding seasons may vary greatly among and within species, within a

population, or even for an individual from year to year. Correspondingly, the control systems that regulate gonadal development appear to show great plasticity of sensitivity to the spectrum of environmental cues known to time breeding seasons. The purpose of this communication is to introduce a concept that may provide a theoretical framework to elucidate mechanisms by which birds, and perhaps other vertebrates, respond to environmental cues that time reproductive events.

THE DIVERSITY OF GONADAL CYCLES

Baker ('38) was the first to point out that breeding seasons at high latitudes tend to be brief (1–3 months) and synchronized with the short summer period when environmental conditions are favorable for raising young and for their survival (Fig. 1). As latitude decreases, favorable conditions persist for longer periods and breeding seasons are correspondingly longer. In equatorial regions, some species can be found breeding at all times of the year (Fig. 1). However, Baker ('38) was careful to point out that this trend should be viewed cautiously since many

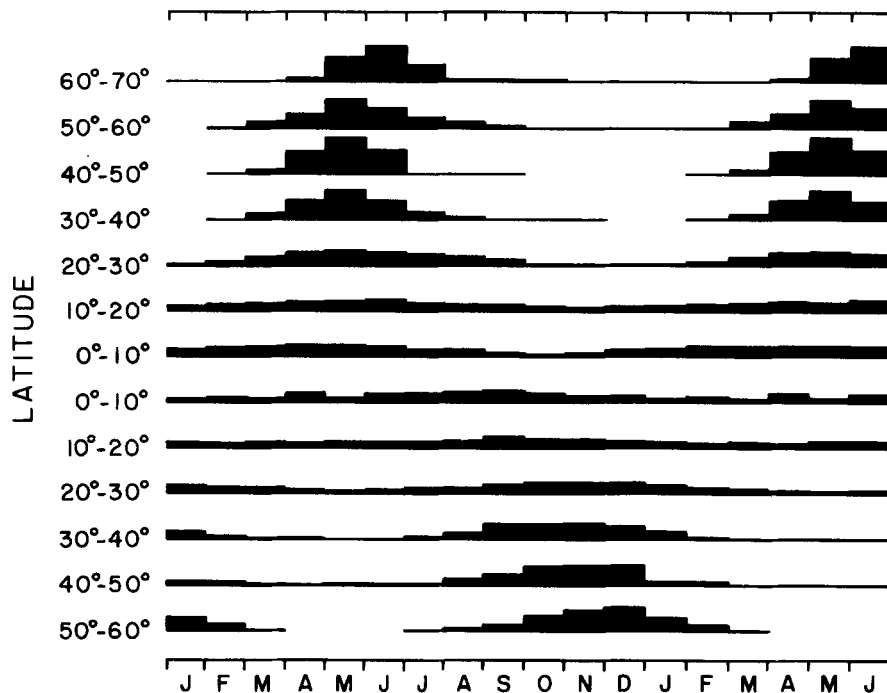


Fig. 1. The relationship of breeding season (indicated by black blocks) with latitude. Full blocks indicate that all or most members of the population are breeding; proportionately smaller

blocks indicate that only part of the population may be breeding at that time. Redrawn from Baker ('38).

tropical species have discrete breeding seasons. Later studies showed that even in species that appear to reproduce at all times of year, individuals may have distinct cycles of gonadal maturation and regression (Miller, '62). Furthermore, although there is a trend for longer breeding seasons toward the tropics, there are noteworthy exceptions suggesting complex interplays of environmental cues and reproductive function in relation to optimal timing of nesting. For example, a few species that breed at high latitudes can have extended breeding seasons, e.g., the rock dove, *Columba livia*, that is capable of breeding year round (Lofts et al., '66). Other species are opportunistic and have also been recorded as breeding in any month. A classic example is the red crossbill, *Loxia curvirostra*, that regularly breeds in winter despite ambient temperatures down to -30°C or lower (Newton, '73). Apparently, breeding in this species coincides with abundant, but erratic, crops of its principle food—the seeds of coniferous trees. The zebra finch, *Poephila guttata*, of the Australian deserts is another opportunist, and is thought to breed whenever sufficient rain results in production of a new crop of grass seeds, insects etc. (Farner and Serventy, '60; Immelmann, '65; Sossinka, '80; Vleck and Priedkalns, '85).

ENVIRONMENTAL REGULATION OF REPRODUCTIVE PERIODICITY

Baker ('38) suggested that there are two ways by which environmental conditions can affect reproductive processes. These are ultimate and proximate factors. Ultimate factors select for individuals that breed at a time most favorable for survival of young. There are several known examples of ultimate factors, but the most ubiquitous is availability of food (e.g., Lack, '68; Immelmann, '71, '73; Perrins, '70). Proximate factors are the environmental cues (see below) that actually regulate reproductive processes from maturation to termination of breeding. These factors act through the neuroendocrine and endocrine systems that in turn control maturation of reproductive organs and development of reproductive behavior.

There is a bewildering array of known and putative proximate factors, perhaps as many as there are species of birds. The primary literature on this topic has been reviewed exhaustively by Marshall ('59, '70), Lofts and Murton ('68), Murton and Westwood ('77), Immelmann ('71, '73), and Brown and Britton ('80), revealing the complexity of potential environmental control systems. At first, the enormity of variation from species to species daunts

any thought of elucidating common basic mechanisms of the hormonal responses and neural pathways by which environmental information is transduced. However, a scheme to classify the roles of proximate factors on reproduction in birds has been proposed recently that provides a simpler way of approaching this overwhelming battery of environmental information in a systematic manner. This scheme serves here as a framework to investigate the mechanisms by which environmental factors influence reproduction (Wingfield, '80, '83; and refined by Wingfield and Kenagy, '91), and is outlined below.

Initial predictive information regulates onset of gonadal development, maintains a physiologic state in which the organism can respond to other environmental cues, and finally precipitates gonadal regression at the end of the breeding season. Such reliable cues are few (e.g., the annual change in day length, endogenous rhythms, see Farner, '85; Gwinner, '87) and initiate a reproductive cycle in anticipation of the breeding season, i.e., they are of predictive value in the *long term*.

Supplementary information fine tunes rate of gonadal maturation, onset of breeding, and its termination according to local phenological conditions. For example, onset of spring can vary from year to year and a host of local conditions such as temperature and availability of food, water, nest sites, etc., can affect gonadal maturation stimulated by initial predictive information. There are two types of supplementary information—accelerators and inhibitors (Marshall, '59, '70)—and they act as predictive information in the *short term*.

Synchronizing and integrating information comprises all of the behavioral interactions, including inter- and intra-sexual, as well as between parents and offspring. These cues synchronize the reproductive effort of a breeding unit and integrate transitions of reproductive behavior, e.g., from sexual to parental phases (see Wingfield and Marler, '88; Wingfield and Kenagy, '91, for detailed reviews).

Modifying information tends to disrupt a reproductive cycle once actual breeding (i.e., nesting) is underway. For example, predators may take the nest and eggs, or a storm may force adults to abandon the nest and young. Renesting usually occurs as soon as conditions ameliorate (see Wingfield, '88, for complete review).

Only initial predictive and supplementary types of factors regulate gonadal maturation and regression on a *seasonal basis*. Note that both provide *predictive* information that allows the individual to prepare for the oncoming breeding season (Farner,

'70). The other two categories can affect gonadal state but may not control *seasonal* cycles. For example, behavioral interactions can synchronize gonadal development within a colony (e.g., Fraser-Darling, '38) or a pair (Lehrman, '65), but these may only operate within a breeding season already precipitated by initial predictive and supplementary cues. Similarly, modifying information may only influence reproductive state after actual nesting has begun (and when gonadal maturation is complete). Very few investigations have addressed the interrelationships of the different types of environmental factors. This communication focuses on the possible mechanisms by which two of these types of factors, initial predictive and supplementary information, are integrated into neuroendocrine and endocrine secretions that in turn regulate gonadal cycles.

Our knowledge of how initial predictive and supplementary cues affect breeding cycles is almost completely restricted to north temperate species. As a result there is a tendency to assume that the annual cycle in day length is "the most important factor" regulating breeding cycles in birds simply because most experimental work has been conducted on photoperiodic mechanisms. There is no question that photoperiod is a very important factor regulating seasonal breeding in many species at mid- to high latitudes (e.g., Farner and Follett, '79; Follett, '84), but since two-thirds of the world's species live and breed at mid- to low latitudes where conditions favorable for breeding may be prolonged but less predictable, an extension of dogma formed from investigations of a few temperate species to the majority is not tenable. For this reason it is proposed here to take a more general look at control of reproductive periodicity, bearing in mind the broad spectrum of problems different species face when timing breeding in diverse and sometimes capricious environments.

To begin, it is pertinent to consider the ultimate factors that provide selection for mechanisms by which environmental information is integrated to regulate cycles of gonadal function. We will then discuss possible theoretical ways to investigate how proximate information may be used to regulate gonadal cycles for optimal timing of breeding.

Several papers in the ecological literature present mathematical approaches for investigating seasonality of flowering and fruiting in plants (e.g., Cohen, '67; Colwell, '74). These papers provide a formal and practical basis for assessment of the *predictability* of an organism's environment. Although this concept has been used in ecological investiga-

tions for years it has not, as far as we are aware, been incorporated into theoretical models of how organisms such as birds regulate physiological changes associated with gonadal cycles. Experimental approaches to determine neuroendocrine and endocrine mechanisms might benefit from such models based on the ecology of the species or population under study, since predictability of changes in an environment will clearly determine the relative value (importance) of long-term (initial predictive) and short-term (supplementary) information from that environment. The relative contributions of initial predictive and supplementary types of information in turn may indicate the extent to which an individual must integrate different cues within the CNS. This latter point also addresses the complexity of perception and neural pathways needed to transduce environmental signals into neuroendocrine secretions that provide a link with the organism's physiology.

THE CONCEPT OF PREDICTABILITY

The most energetically expensive (rate limiting) phase of a reproductive cycle is the provision of food for the offspring (e.g., Lack, '68). Thus ultimate factors such as availability of food select for those individuals that produce young at a time when trophic resources can support such a high rate of provision-

ing. Clearly, predictability of the ultimate factor is crucial for determining when and how an individual prepares for the breeding season. Colwell ('74) developed a mathematical model that allows us to ascribe a predictability value (**Pr**) to any resource. Colwell ('74) also recognized two components of predictability: *constancy* (**C**), the uniformity of resource levels across time intervals within a year; and *contingency* (**M**), the degree of fluctuation in resource levels across time intervals within a year. The value of **Pr** can vary between 0 (entirely unpredictable) and 1 (entirely predictable), and is equal to the sum of the separate components **C** and **M**. The critical features of this model with respect to control of reproductive physiology are the total **Pr** and the relative contributions of the separate components **C** and **M**.

If the resource for feeding young (ultimate factor) is known, then it is possible to apply Colwell's ('74) formulas and calculate a **Pr** value for a population utilizing that resource. To do this we set up frequency matrices (see Table 1) with **t** columns (times within a cycle, e.g., seasons, months of the year etc.) and **s** rows (states of the phenomenon, e.g., low food, high food, breeding, non-breeding). To illustrate the application of this model, we have constructed hypothetical matrices of season and trophic resources in imaginary environments (Table 1):

TABLE 1. Frequency matrices for trophic level and season in hypothetical environments¹

Environment a					Environment b				
	W	Sp	Su	A		W	Sp	Su	A
I	0	0	0	0	I	12	0	0	0
II	0	0	0	0	II	0	0	0	12
III	0	0	0	0	III	0	0	12	0
IV	12	12	12	12	IV	0	12	0	0
Pr = 1, C = 1, M = 0					Pr = 1, C = 0, M = 1				
Environment c					Environment d				
	W	Sp	Su	A		W	Sp	Su	A
I	0	0	0	0	I	0	0	0	0
II	12	0	0	0	II	2	0	0	1
III	0	0	0	12	III	10	2	10	11
IV	0	12	12	0	IV	0	10	2	0
Pr = 1, C = 0.25, M = 0.75					Pr = 0.71, C = 0.44, M = 0.27				
Environment e					Environment f				
	W	Sp	Su	A		W	Sp	Su	A
I	4	0	0	0	I	3	3	3	3
II	4	0	0	4	II	3	3	3	3
III	4	1	9	8	III	3	3	3	3
IV	0	11	3	0	IV	3	3	3	3
Pr = 0.53, C = 0.12, M = 0.41					Pr = 0, C = 0, M = 0				

¹The columns (t) represent seasons where W = winter; Sp = spring; Su = summer; and A = autumn. The row (s) represent trophic levels in the hypothetical environments a-f. I = no trophic resources; II = resources sufficient for maintenance; III = resources above maintenance threshold but not sufficient for breeding; IV = trophic level sufficient for breeding. Predictability (Pr), constancy (C), and contingency (M) were calculated after Colwell ('74). See text for further details.

Let **t** (columns) = time of year (or seasons) where W = winter (December 21–March 20), Sp = spring (March 21–June 20), Su = summer (June 21–September 20), and A = autumn (September 21–December 20). Let **s** (rows) = trophic level in the environment where I = no trophic resources, II = trophic level sufficient for body maintenance, III = trophic level above threshold for body maintenance but below that required to feed young, and IV = trophic level at or above that necessary for production of a clutch of eggs and for provisioning of young.

If we assume (arbitrarily) 12 years of data, then frequency matrices for trophic resources at different times of the year can be constructed with the number of years that resources were at each level entered in each cell of the matrix, and predictability, constancy, and contingency can be calculated. For example, in hypothetical environment **a** (Table 1), trophic level is sufficient for breeding in every season of the year and thus predictability (**Pr**) = 1 and is due to constancy (**C** = 1) rather than contingency (**M** = 0). In environment **b**, **Pr** is also equal to 1, but trophic resources vary maximally and are sufficient for breeding only at one season in each year. In this case **Pr** is due entirely to contingency (**C** = 0, **M** = 1). On the other hand, in environment **c**, **Pr** = 1 but is due partially to constancy and contingency (**C** = 0.25, **M** = 0.75). Thus a given predictability value can comprise any combination of constancy and contingency. In environment **a** constancy is high and conditions are always favorable for breeding. Thus it is possible that a population utilizing this resource will either always have gonads in a functional, or near functional, state, or reproductive function depends entirely on endogenous factors such as age and body condition. Predictive information of any type (initial predictive or supplementary) may be of little use in this environment. In contrast, environments **b** and **c** (Table 1), have trophic levels sufficient for breeding only during discrete periods of the year. In these cases there is a high contribution of contingency to the predictability values (the constancy component is therefore low). Because of the strong seasonality in these resources, populations utilizing them may undergo marked gonadal recrudescence in anticipation of onset of breeding. As a result, individuals must use environmental cues to time gonadal development in anticipation of the breeding season. Thus a high contribution of contingency indicates sensitivity to environmental cues that pro-

vide predictive information. These data suggest that the relative contributions of constancy and contingency can provide critical information on the extent to which individuals utilizing that resource should integrate environmental signals and use this information to regulate reproductive function.

In environments **d** and **e** the trophic level is not completely predictable in every season (Table 1). In these cases **Pr** is less than 1, although the contribution of **C** and **M** may still vary thus providing useful information on how organisms using these resources should regulate gonadal function. Cohen ('67) has shown mathematically that if a future event (e.g., onset of breeding) is certain in terms of timing, then it is optimal to respond to one or a few reliable environmental cues and ignore others. On the other hand, if the future event (onset of breeding) is less certain in terms of timing, then receiving more information about potential alternative decisions (i.e., inhibit or accelerate gonadal maturation) can only lead to finer tuning of onset of breeding with local phenological conditions. Thus as predictability decreases, then more information, especially concerning local conditions, should be needed to time physiological changes and onset of breeding appropriately. Finally, in environment **f**, any trophic level is equally likely at any time of year and thus **Pr** = 0 (and **C** = 0 and **M** = 0, Table 1). In this last case we would expect populations using these resources to make physiologic adjustments opportunistically by responding only to short-term (supplementary) cues.

In this way it is possible to apply the contingency/constancy model of predictability to data on changes in ultimate factors and calculate **Pr**, **C**, and **M**. These values then provide specific information on how we would expect individuals within a population under study to respond to the environment, and how they might integrate environmental signals to time the breeding season optimally. Despite the potential usefulness of this approach, actual data on ultimate factors such as trophic levels throughout a year are few and difficult to obtain and interpret. For example, an ultimate factor such as a specific food resource fed to young (e.g., insects) may only be present for a short time. In this case, general trophic level (i.e., all foods combined) would not be appropriate for predicting breeding seasons (although it would still provide salient information for strategies of migration, hibernation, etc.). Another complication is that food may not be the only ultimate factor. In some cases onset of breeding may not occur because high rates of predation reduce reproductive success even though trophic levels are

favorable (e.g., Morton, '71; Brown and Britton, '80). Other factors may also be important (see Immelmann, 71, 73). Therefore, knowledge of several specific ultimate factors that select for periodic breeding may be required in order to collect the relevant data for a given species or population. One way to circumvent this problem might be to substitute time of year when clutches are initiated for the species or population of interest. Such data are more widespread in the literature and relatively easy to obtain. This approach may have a significant advantage in that it would not make any assumptions about what the ultimate factors constraining breeding are. However, predictability of several ultimate factors would be implicit in our calculations. Using the time of clutch initiations to construct the matrices could be a powerful way to predict the sensitivity of individuals to environmental factors that regulate gonadal development and function.

To do this requires a different format for the matrix:

Let t (times in the cycle) = months of the year (January through December), and let s (states) = no clutches initiated (i.e., no clutches of eggs laid in that month) or clutches initiated (i.e.,

clutches of eggs laid in that month). A number of examples are given using actual data from the literature and unpublished observations (Tables 2, 3).

It should be noted here that increasing t (times in a cycle) greatly enhances the resolution of \mathbf{Pr} , \mathbf{C} , and \mathbf{M} . If seasons are used, then resolution is lost because some species may breed only for 1 month within a season. Moreover, if a population has a breeding season that spans late spring and early summer, then the breeding season may appear to be 6 months long rather than just 1 month long! Months provide a much more detailed summary of events over a year. Such information collected over several years can provide a frequency matrix allowing calculations of \mathbf{Pr} , \mathbf{C} , and \mathbf{M} for the species or population under study. This information can then be used to predict the likely pattern of gonadal recrudescence and regression, and the way in which environmental cues (i.e., initial predictive and supplementary information) may be utilized and integrated to time gonadal development and regression.

Since real data will be used it is possible to calculate a G statistic for \mathbf{Pr} , \mathbf{C} , and \mathbf{M} (Colwell, '74) and ascribe significance levels to predictability and

TABLE 2. Frequency matrices for breeding seasons in sparrows of the genus *Zonotrichia*¹

	J	F	M	A	M	J	J	A	S	O	N	D
White-crowned sparrow, <i>Z. l. gambelii</i> , central Alaska												
No clutches	4	4	4	4	2	0	3	4	4	4	4	4
Clutches present	0	0	0	0	2	4	1	0	0	0	0	0
Predictability = 0.85 (Gp = 56.5, $P < .005$); contingency = 0.45 (Gm = 29.8, $P < .005$); constancy = 0.40 (Gc = 26.7, $P < .01$) Ie factor = 1.13												
White-crowned sparrow, <i>Z. l. pugetensis</i> , W. Washington												
No clutches	6	6	6	3	0	0	2	5	6	6	6	6
Clutches present	0	0	0	3	6	6	4	1	0	0	0	0
Predictability = 0.79 (Gp = 78.4, $P < .005$); contingency = 0.64 (Gm = 63.7, $P < .005$); constancy = 0.15 (Gc = 14.7, $P > .1$) Ie factor = 4.27												
White-crowned sparrow, <i>Z. l. nuttalli</i> , central California												
No clutches	5	5	4	1	0	0	3	3	5	5	5	5
Clutches present	0	0	1	4	5	5	2	2	0	0	0	0
Predictability = 0.72 (Gp = 59.7, $P < .005$); contingency = 0.62 (Gm = 51.4, $P < .005$); constancy = 0.099 (Gc = 8.26, $P > .5$) Ie factor = 6.26												
Song sparrow, <i>Z. melodia morphna</i> , W. Washington												
No clutches	3	3	2	0	0	0	1	2	3	3	3	3
Clutches present	0	0	1	3	3	3	2	1	0	0	0	0
Predictability = 0.77 (Gp = 38.4, $P < .005$); contingency = 0.71 (Gm = 35.6, $P < .005$); constancy = 0.056 (Gc = 2.8, $P > .9$) Ie factor = 12.7												

¹The columns (t) represent months of the year and the rows (s) represent breeding status, i.e., whether clutches were initiated (clutches present) or not (no clutches). Predictability, contingency, and constancy were calculated according to Colwell ('74). Gp = G statistic for predictability; Gm the same for contingency (m); and Gc the same for constancy (c). Degrees of freedom = $t(s - 1) = 12$. Environmental information factor (the No. representing sensitivity to environmental cues = Ie) is the ratio of contingency to constancy (M/C). The tables were constructed from information provided in Blanchard ('41); Blanchard and Erickson ('49); King et al. ('66); Mewaldt and King ('77); Wingfield and Farner ('78); and J.C. Wingfield (unpublished observations).

TABLE 3. Frequency matrices of breeding seasons with high constancy or contingency¹

	J	F	M	A	M	J	J	A	S	O	N	D
Rock Dove, <i>Columba livia</i> , north temperate zone												
No clutches	2	1	1	0	0	0	0	0	0	0	1	2
Clutches present	10	11	11	12	12	12	12	12	12	12	11	10
Predictability = 0.79 (Gp = 157.3, $P < .005$); contingency = 0.07 (Gm = 13.7, $P > .1$); constancy = 0.72 (Gc = 143.6, $P < .005$) Ie factor = 0.095												
Sooty tern, <i>Sterna fuscata</i> , Ascension Island												
No clutches	9	12	11	10	11	10	12	10	11	12	9	12
Clutches present	3	0	1	2	1	2	0	2	1	0	3	0
Predictability = 0.6 (Gp = 119.5, $P < .005$); contingency = 0.08 (Gm = 16.1, $P > .1$); constancy = 0.52 (Gc = 103.4, $P < .005$) Ie factor = 0.15												
Darwin's Ground Finch, <i>Geospiza sp.</i> , Galapagos Islands												
No clutches	0	0	1	1	2	3	3	3	4	4	4	2
Clutches present	4	4	3	3	2	1	1	1	0	0	0	2
Predictability = 0.50 (Gp = 33, $P < .005$); contingency = 0.48 (Gm = 32, $P < .005$); constancy = 0.01 (Gc = 0.75, $P > .1$) Ie factor = 42.8												

¹The columns (t) represent months of the year and the rows (s) represent breeding status, i.e., whether clutches were initiated (clutches present) or not (no clutches). Predictability, contingency, and constancy were calculated according to Colwell ('74). Gp = G statistic for predictability; Gm the same for contingency (m); and Gc the same for constancy (c). Degrees of freedom = $t(s - 1) = 12$. Environmental information factor (the No. representing sensitivity to environmental cues = Ie) is the ratio of contingency to constancy (M/C). The tables were constructed from information provided in Lofts et al. ('66), Chapin ('54), Gibbs and Grant ('87), Boag and Grant ('84), and J.C. Wingfield (unpublished observations).

its components. The P value does not address the significance of the value of C or M per se, but indicates whether C or M contribute significantly to the overall Pr value for the number of years for which data are available. In Table 2 we present frequency matrices for breeding in 4 taxa of *Zonotrichia* sparrows. Note that although Pr is reduced as latitude of breeding decreases (reflecting that onset and termination of breeding are more variable at lower latitudes), the relative contributions of M and C vary even more markedly. This indicates that the ratio of M to C is important as well as Pr . All three values together provide the most sensitive measure of variability in onset of breeding. Table 3 presents frequency matrices of breeding data from species that breed more or less continuously (rock dove, and sooty tern, *Sterna fuscata*), or have a more variable breeding season (Darwin's ground finches, *Geospiza sp.*). Again, although Pr values vary, the ratio of M to C is also a good indicator of variations in breeding periods. The breeding seasons of the rock dove and sooty tern show high predictability that is due entirely to constancy (contingency is not a significant factor, Table 3). Darwin's ground finches also have a significant Pr value, but this time due entirely to contingency (constancy is not a significant factor, Table 3).

What, then, do Pr , C , and M tell us about patterns of gonadal development and environmental control of breeding, and how can we use these values to gain insight into mechanisms by which

organisms respond to environmental signals? Clearly the ratio of M to C varies greatly among the examples given in Tables 2 and 3. The total Pr is important because it indicates whether an organism will be able to *rely* on conditions being favorable for breeding at a certain time of year. If a future event (such as onset of breeding) is predictable (high Pr), we could argue (based on Cohen '67, see above) that very reliable cues such as photoperiod (i.e., initial predictive information—long term) would predominate. On the other hand, if timing of the future event, i.e., the breeding season, is less certain (decreasing Pr), then receiving more information about potential alternative decisions can only lead to finer tuning of onset of breeding with local phenological conditions. Thus, in these cases supplementary information of local origin, and predictable in the short term, may be used to inhibit or accelerate gonadal maturation in conjunction with initial predictive cues. However, as Pr decreases further, the contribution of initial predictive information may also decrease and supplementary cues would predominate.

As Pr increases, the contributions of C and M become more significant. For instance, at high Pr values it is important to know whether the breeding season is predictable because of constancy, contingency, or a combination. Obviously, the integration of environmental cues timing reproductive function will be different depending on whether C or M predominates (i.e., the M/C ratio). Therefore, relative values of Pr , C , and M are important

and, taken together, provide what we have dubbed an *environmental information factor*, I_e . Based on the above relationships, we can argue that I_e is proportional to the M/C ratio controlled for variations in Pr . We can express this relationship as:

$$I_e = \frac{M/Pr}{C/Pr} = \frac{M}{C}.$$

We suggest that I_e be used as an indicator of the types of environmental information an individual requires to optimize onset of breeding (Fig. 2). The actual value of I_e should not be interpreted as indicative of the number of cues used, but rather as a measure of the relative contribution of initial predictive and supplementary types of information that in turn indicates the way in which organisms *integrate* these environmental signals. Figure 2 illustrates how curves representing changes in the contributions of initial predictive and supplementary types of information can be used to reveal relationships with I_e . The contribution of types of environmental information needed to optimize timing of breeding is the sum of initial predictive information (IPI %) and supplementary information (SI %).

This approach is testable. At low I_e (<1), C predominates and M is less important. In this case we expect that initial predictive information should predominate. At very low I_e values (close to 0), perhaps little or no environmental information is

required to *time* gonadal maturation since conditions are always suitable for breeding. When $I_e = 1$, then C and M make equal contributions. Here we argue that both initial predictive and supplementary types of information need to be integrated. Individuals with such I_e values may be sensitive to several environmental cues that influence secretion of reproductive hormones and thus gonadal maturation. When I_e is high (>1), M becomes greater than C and we expect supplementary information to predominate, although some integration with initial predictive information may be important. At very high I_e values, M predominates and supplementary information may be the major type of environmental cue important for regulating breeding. Such environments may be unpredictable and thus opportunistic breeding would be the common strategy. It is logical to conclude that in the latter habitats long-term predictive cues (such as initial predictive information) may be of little or no use.

This approach may have value in comparing populations with different I_e values and in designing tests of their responses to initial predictive (e.g., photoperiod) or supplementary (e.g., temperature, food availability) types of environmental information. We next examine the existing evidence for physiological mechanisms as they relate to variations in I_e factors as preliminary evidence against, or in support of, the model in general.

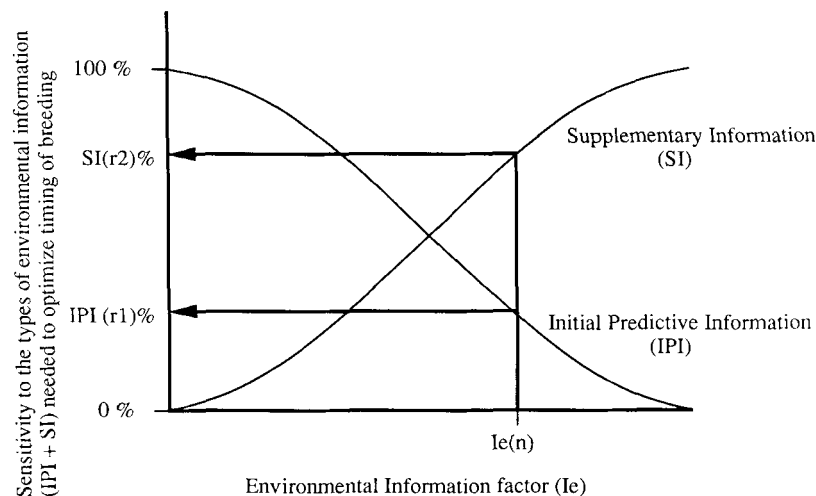


Fig. 2. Theoretical relationships of the environmental information factor (I_e) and the relative contribution of types (initial predictive information, IPI , and supplementary information, SI) of environmental information needed to optimize timing of breeding. I_e is the ratio of contingency (M) to constancy (C).

Note that as I_e tends to zero the individual may respond only to initial predictive information. As I_e increases, supplementary information becomes important. At very high I_e values, supplementary information may predominate.

ENVIRONMENTAL CONTROL OF GONADAL CYCLES WHEN CONSTANCY IS HIGH

When constancy is high, I_e is low (<1). Our argument is that under these conditions individuals are most sensitive to initial predictive information for timing reproductive events. Supplementary information is less important, although it may be useful immediately prior to onset of breeding for very fine tuning effects. When I_e is extremely low (close to 0) then it could be argued that the environment is so constant that little, if any, information is needed. Environments that are constant and in which breeding can always occur are rare. Some tropical rainforests appear constant in terms of rainfall, temperature etc. Nonetheless, food resources can fluctuate and many species exhibit periodic breeding. In some populations breeding can be found at all times of year (e.g., *Zonotrichia capensis* in Columbia—Miller, '62), but when individuals are monitored it is clear that each has a discrete period of breeding and non-breeding. Only the male and female of a breeding pair are synchronized. Miller ('62) found that individual male, *Z. capensis* underwent two testicular cycles a year coincident with two periods of breeding.

Although data from apparently constant environments should be treated with caution, some islands in the southern Pacific Ocean, e.g., Ascension Island, have relatively constant conditions and sup-

port continuous breeding. Supplies of fish appear to be always above the threshold required for local sea birds to feed young successfully. Chapin ('54) and later Ashmole ('63) found that sooty terns breed at all times of year. However, each colony is synchronous in timing of egg-laying, but the cycle of breeding, followed by a molt, requires about 9 months (Fig. 3). Application of the contingency/constancy model of predictability to the breeding data given in Chapin ('54) gives an I_e factor of 0.15 (Table 3). In this instance it could be argued that initial predictive information should be more important than supplementary types of information for timing breeding. In Figure 3 it can be seen that breeding cycles of individual colonies of sooty terns appear to "free-run" and are not tied to any annual cycle. Thus it is possible that an endogenous period of about 9 months (the time required to breed once and then molt) regulates timing of breeding. Note, however, that synchronizing and integrating factors may be important for within colony synchrony. Bad weather (e.g., a typhoon, a modifying factor) may disrupt breeding, but under normal conditions breeding can progress continuously.

The rock dove is another example of a species capable of continuous breeding. This species is a commensal of humans and can feed on a wide spectrum of foods. Even in cities and farms of the northern hemisphere, where seasonal changes in temperature, day length, and rainfall can be ex-

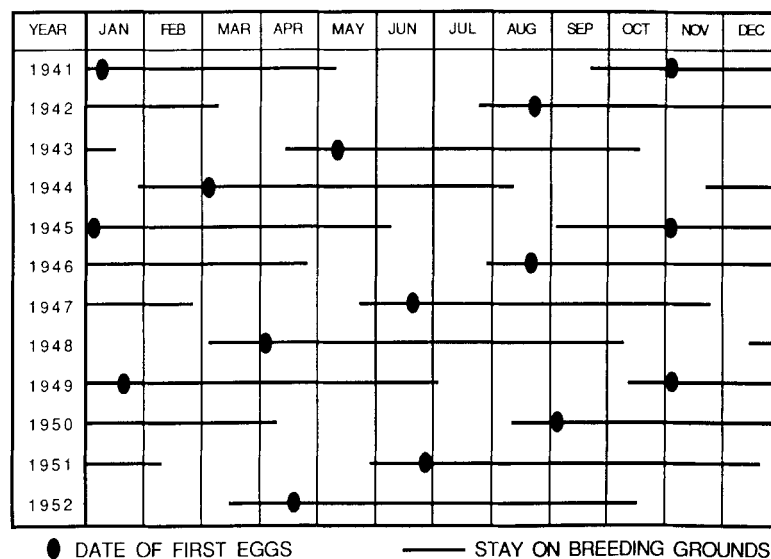


Fig. 3. Nesting schedule of the sooty tern (*Sterna fuscata*) on Ascension Island. Redrawn from Chapin ('54).

treme (i.e., cold winters and warm summers), these birds can breed all year since food (the ultimate factor) around human habitations is always abundant (Murton et al., '72). Furthermore, rock doves process food and feed their young on crop milk thus freeing the adults from having to collect specialized foods as do other birds. In Table 3 it can be seen that the *Ie* factor for this species is very low (0.097) indicating that sensitivity to environmental cues timing breeding may be low. Indeed, Lofts et al. ('66) showed that gonadal state in rock doves is not influenced by photoperiod. Thus, although much more experimental investigation is needed, it does appear that "continuous breeders" may rely more on body condition, age, etc., rather than environmental information to regulate reproductive function.

ENVIRONMENTAL CONTROL OF GONADAL CYCLES WHEN CONTINGENCY AND CONSTANCY MAKE SIMILAR CONTRIBUTIONS TO PREDICTABILITY

When *M* and *C* make more or less equal contributions to *Pr*, then *Ie* will be close to 1. Now we would expect initial predictive information to still predominate, but supplementary cues also to play a role, especially for fine-tuning onset of breeding. These environments are seasonal (because *M* is a significant contributor), and as a result breeding seasons are usually restricted. Such reproductive cycles are almost ubiquitous at higher latitudes and may also be widespread in tropic regions in which rainy seasons are well defined and limited. Many species are migratory and initiate gonadal development on a wintering ground far removed from the breeding area. In these cases, individuals must be able to select and respond to those environmental events that convey relevant information about phenologic progression on the breeding ground and ignore all other events (Cohen, '67). Only when on the breeding ground do supplementary factors (local information, predictive in the short term) become important.

A migrant far from its breeding ground has few options. For example Gambel's white-crowned sparrow, *Zonotrichia leucophrys gambelii*, breeds in the arctic and sub-arctic regions of North America where summers are brief but predictable. This species has been investigated in detail and rapid gonadal development in response to increasing day length has been well established (see Farner, '86, for review). In Table 2, breeding data for *Z. l.*

gambelii are presented and the *Ie* factor is 1.13. In this taxon, it could be concluded that initial predictive information (photoperiod) provides accurate information, and all other cues may be irrelevant until actually on the breeding ground. Experimental evidence supports this conclusion since the effects of supplementary cues such as low environmental temperature and restricted food are ineffective in suppressing the response to photoperiod (e.g., Farner and Lewis, '71, '73; Wingfield, '88; Wingfield et al., '82). Thus this taxon of white-crowned sparrow conforms with the suggestion that if *Ie* is close to 1 then initial predictive cues should predominate. Supplementary information becomes important only when on the breeding ground and fine-tunes onset of breeding to local conditions.

In other long-distance migrants (e.g., the *Sylvia* warblers of Europe), photoperiod may act to *entrain* strong endogenous rhythms of gonadal maturation, regression, molt, and migration (e.g., Berthold, '88; Gwinner, '87). Even for birds that are sedentary, but have very restricted breeding seasons, if the future event (time of breeding) is certain (*M* is significant) then it is optimal to respond maximally to one or few cues (e.g., photoperiod or endogenous rhythm). This contrasts dramatically with an apparent free-running rhythm of breeding (i.e., absence of entrainment by an external environmental cue) in the sooty term (Fig. 3).

ENVIRONMENTAL CONTROL OF GONADAL CYCLES WHEN THE CONTRIBUTION OF CONTINGENCY IS GREATER THAN THAT FOR CONSTANCY

As the relative contribution of *M* to *Pr* increases, we suggest that initial predictive and supplementary types of information are important as *Ie* increases above 1 (Fig. 2). According to Cohen ('67), if the future event (onset of breeding) is less certain in terms of timing, then receiving more information about potential alternative decisions (i.e., inhibit or accelerate gonadal development) can only lead to finer tuning of gonadal maturation with local phenologic conditions. Thus as onset of breeding and the rate of gonadal maturation show greater degrees of variation within a year and from year to year, the *Ie* factor increases (e.g., for *Zonotrichia* sparrows at lower latitudes, Table 2).

The empirical evidence available tends to support the prediction that as *Ie* increases, then initial predictive and supplementary types of information need to be integrated. For example, if we

compare a population of song sparrow, *Zonotrichia melodia*, breeding in New York State (42°N), with a population of *Z. l. gambelii* migrating from a wintering ground in San Diego (southern California, 31°N) to a breeding ground in central Alaska (64°N, Fig. 4), the ambient temperatures experienced by these two taxa in spring are markedly different (Fig. 5). Song sparrows experience slowly increasing temperatures throughout the period of gonadal maturation in spring. Thus, local conditions such as temperature are meaningful to this species that is already on its breeding ground. In contrast, *Z. l. gambelii* experiences steadily declining temperatures as it migrates north (when most gonadal maturation takes place). Only when *Z. l. gambelii* reaches its breeding ground do temperatures begin to increase. In this case ambient

temperature during migration (when gonadal development occurs) is irrelevant as an indicator of conditions on the breeding grounds, and reliance on initial predictive cues (e.g., photoperiod) rather than supplementary cues is probably favored. From these observations we can suggest that migratory species, and those with very precise breeding seasons, would be less responsive to supplementary cues than sedentary species and those with less precise reproductive seasons. The *I_e* factors calculated from breeding data for several taxa of *Zonotrichia* with sedentary and migratory forms (Table 2) support this view.

Reviewing the rather sparse literature, it does appear that low environmental temperature is less effective in suppressing photoperiodically induced testicular growth in migratory species than non-

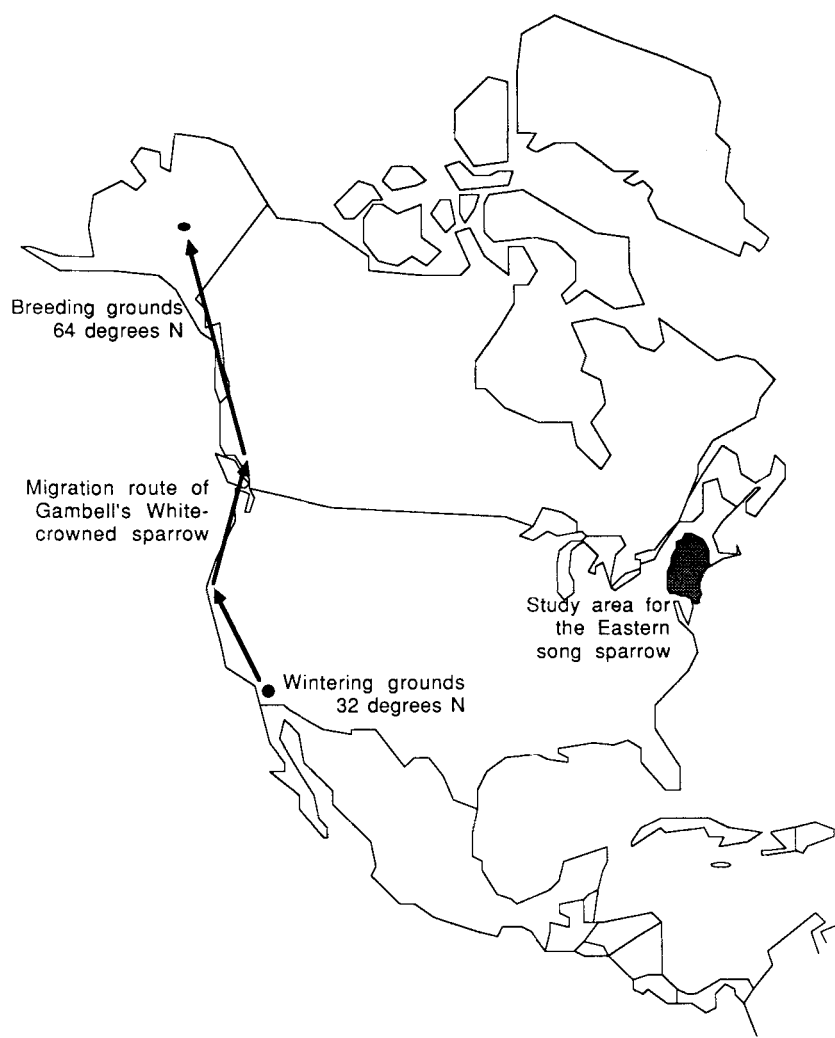


Fig. 4. Map of North America showing the location of the study area for the eastern song sparrow, *Zonotrichia melodia*

and the migratory route of Gambell's white-crowned sparrow, *Zonotrichia leucophrys gambelii*.

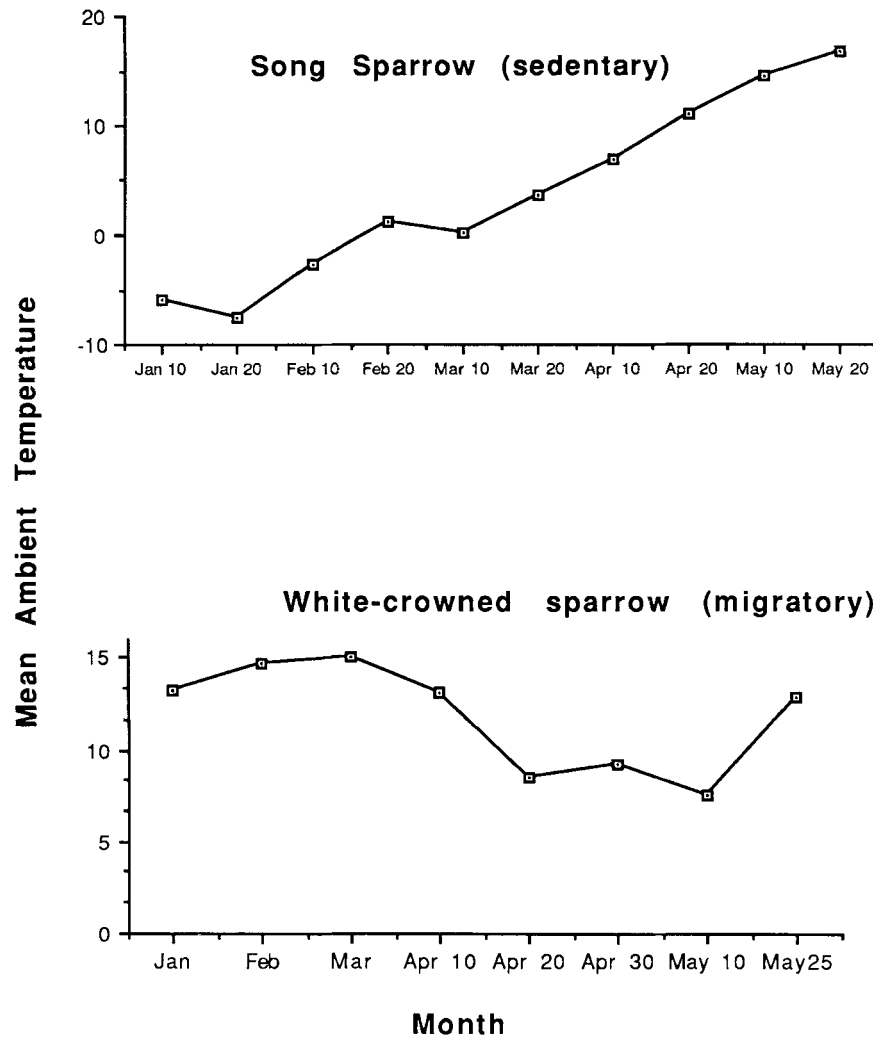


Fig. 5. Changes in ambient environmental temperature during gonadal recrudescence in free-living populations of the song sparrow, *Zonotrichia melodia melodia* in New York (42°N); and white-crowned sparrow, *Zonotrichia leucophrys gambelii*, migrating from its wintering ground in southern California (31°N) to

its breeding ground in central Alaska (64°N). Points represent 30 year means for each date and locality (U.S. Meteorological Survey). Note that for the lower panel, the mean temperatures are presented for each locality that the white-crowned sparrow migrates through en route to Alaska.

migratory species (Fig. 6). Moreover, in the song sparrow, rates of testicular recrudescence were variable from year to year with retarded maturation in cold versus warm springs (Fig. 7). This is in contrast to the highly migratory *Z. l. gambelii* that exhibited very similar rates of gonadal recrudescence in three different field studies in different years (Fig. 7). These data support the hypothesis (Fig. 2) that if the *Ie* factor is low then individuals respond to initial predictive information predominantly and ignore (are insensitive to) other supplementary information until on the breeding ground. However, as the *Ie* factor increases, apparently more information is needed to regulate gonadal

maturation and optimize timing of breeding with local phenology. In this case, an interplay of both initial predictive and supplementary cues becomes important.

ENVIRONMENTAL CONTROL OF GONADAL CYCLES WHEN THE CONTRIBUTION OF CONTINGENCY IS VERY HIGH

When the contribution of *M* to *Pr* greatly exceeds that of *C*, the *Ie* factor becomes very high. Thus supplementary information predominates and a role for initial predictive information declines (Fig. 2). In many cases the trophic resource for breeding is less predictable and opportunistic breeding may

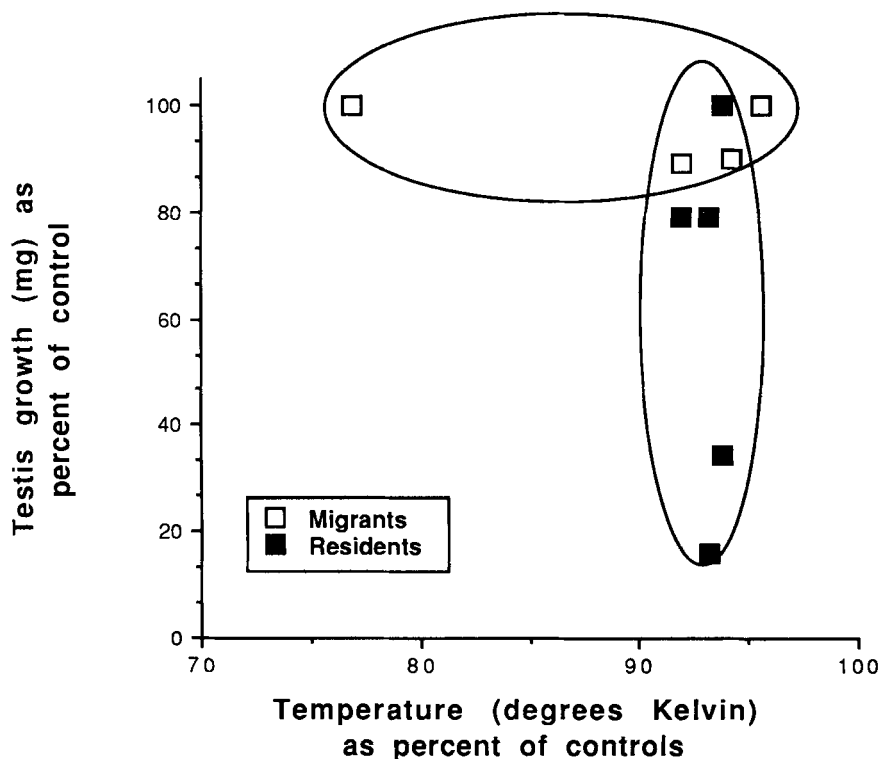


Fig. 6. Effects of reduced ambient temperature on photo-periodically induced testicular maturation in resident and migratory taxa of birds. The experimental (reduced) temperature is expressed as percent of the control in degrees Kelvin. Gonadal growth in the experimental group (exposed to low temperature) is expressed as a percent of the control gonadal growth. Note

that resident species tend to show more inhibition of gonadal maturation than migrants when exposed to reduced ambient temperature. Compiled from Rowan ('25), Suomalainen ('37), Kendeigh ('41), Farner and Mewaldt ('52), Engels and Jenner ('56), Lewis and Farner ('73), Storey and Nicholls ('82), Jones ('86), Wingfield ('88).

be widespread. When **Pr** becomes insignificant (low) then the **Ie** factor is meaningless. In this case it is intuitively obvious that opportunistic breeding would be an appropriate breeding strategy and that initial predictive information would be of little or no use. Examples of opportunists that have been studied in detail are few, but the data available are summarized below.

In the zebra finch, gonads mature after about 60 days of age and may remain in a functional, or near functional, state throughout the individual's life (Farner and Serventy, '60; Sossinka, '80). Breeding is triggered by unpredictable rainfall, and nest building can ensue within hours (Immelmann, '65; Vleck and Preidkalns, '85). Thus initial predictive information would be of little or no use for opportunistic breeders. It should be noted, however, that long-term data from opportunistic populations of zebra finches in the field are lacking, and more investigation is required to confirm the statements above.

The red crossbill, *Loxia curvirostra*, is another example of an opportunistic species. Populations have been recorded as breeding in all months of the

year regardless of temperature and day length (see Newton, '73). Unlike the zebra finch, however, red crossbills do undergo periods of gonadal maturation and regression (Berthold and Gwinner, '78; T.P. Hahn, unpublished data). Whether this is independent of a purely annual cycle remains to be determined. Supplementary factors such as food appear to be critical, and temperature may be of lesser importance, except as it may influence food requirements to reproduce in winter. Tordoff and Dawson ('65) obtained only a weak response in testicular growth from photostimulated red crossbills. On the other hand, Berthold and Gwinner ('78) present evidence for a possible endogenous rhythm of testicular growth in a free-living population of red crossbills in Europe, although the evidence is tenuous. Two other species (tricolored blackbird, *Agelaius tricolor*, and Pinon jay, *Gymnorhinus cyanocephalus*) occasionally exhibit opportunistic breeding in the autumn, although normally they breed in spring. Both species show clear responses to increasing day length in spring, whereas food availability appears to be primarily responsible for stimulating

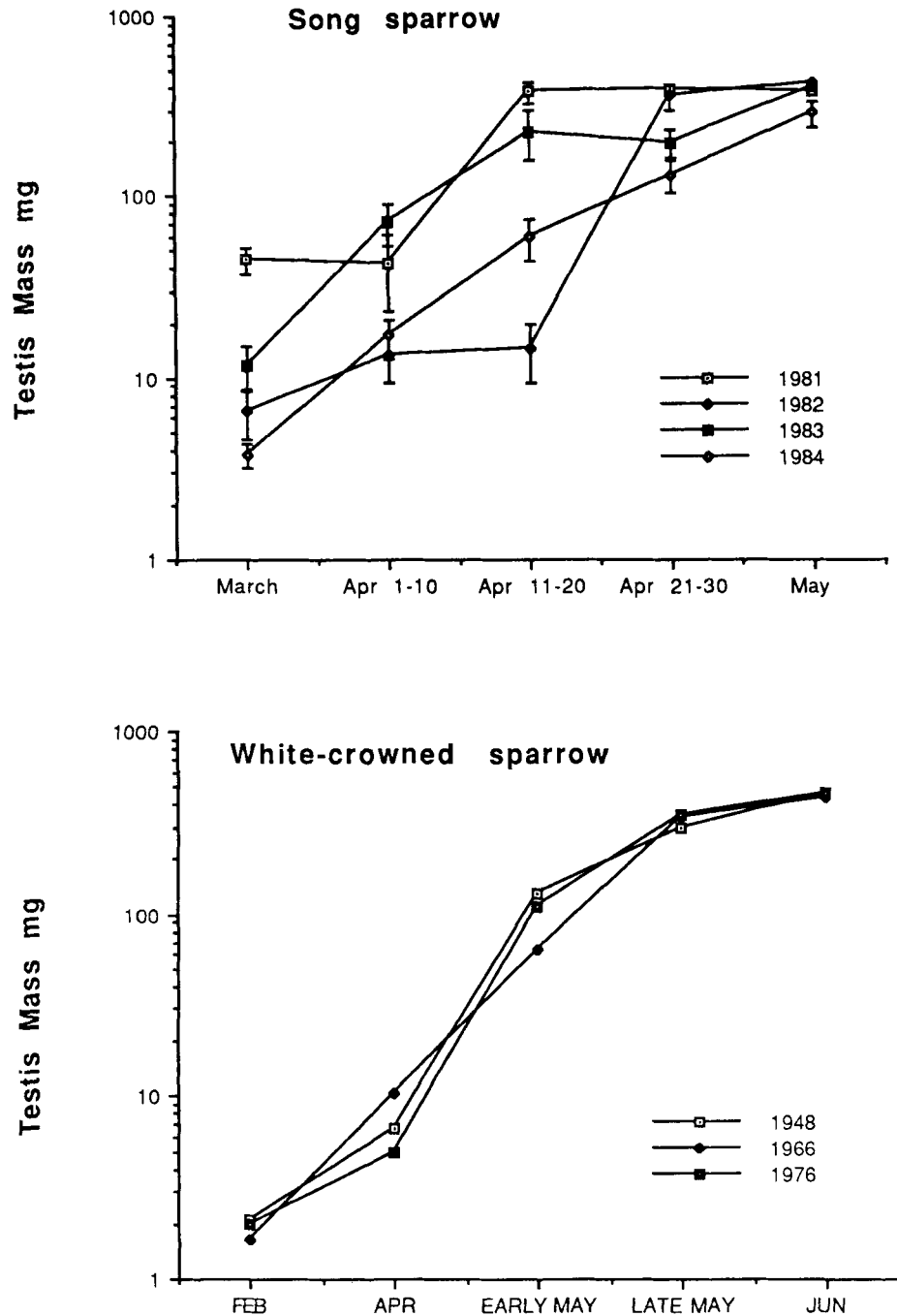


Fig. 7. Variation in the rates of testicular recrudescence in free-living populations of the song sparrow, *Zonotrichia melodia melodia*, resident on its breeding ground (42°N in New York State) during maturation, and white-crowned sparrow, *Zonotrichia leucophrys gambelii*, that undergoes gonadal development

during migration (up the Pacific coast of North America) before reaching the breeding ground in central Alaska (64°N). Data compiled from Blanchard and Erickson ('49), King et al. ('66), and Wingfield and Farner ('78).

gonadal maturation in autumn (Payne, '69; Ligon, '71, '74, '78).

Opportunistic breeding, especially at lower latitudes, may be widespread. Some species apparently breed during the same restricted period for many

years, but then respond immediately should ideal conditions persist, or occur at an unusual time. In Darwin's ground finches, individuals breed during the rains in February every year. However, during a climatic upheaval due to the shifting of a Pacific

Ocean current called El Niño, heavy rains fell for almost 1 year and the finches continued to breed for 9 months or even longer (Gibbs and Grant, '87). In Table 3, it can be seen that the **Ie** factor for this population is very high suggesting predominant reliance upon supplementary information (Fig. 2). Another example is a population of the moorhen, *Gallinula chloropus*, at a farm in South Africa that was able to breed continuously for 4 years by feeding on an artificial high protein diet fed to local ducks. In contrast, a population on a pond 2 km distant, and with no supplemental food, were seasonal breeders (Siegfried and Frost, '75).

Truly random environments (as modeled in Table 1) and absolute opportunism may not exist in nature. Indeed it appears thus far that so called opportunistic breeders actually have a predictable component to their breeding cycle that may be dependent upon initial predictive information. However, this component can be easily over-ridden when unexpected favorable conditions occur (in other words supplementary information predominates). Nevertheless, opportunists may be ideal subjects for testing the contingency/constancy model of predictability for very high **Ie** factors, and may reveal mechanisms for responses to supplemental information that are fundamental for control of relatively flexible breeding seasons in many other species.

CONCLUSIONS: ENVIRONMENTAL INFORMATION FACTORS AND REGULATION OF AVIAN BREEDING CYCLES

We have applied a mathematical model to data on breeding seasons of birds and attempted to use it to gain insight into how populations integrate environmental signals and optimize timing of breeding. Colwell ('74) presented a theory of predictability and applied it to data on plants. However, the principles of the model are easily extended to regulation of breeding seasons in birds. This modified form of the theory assumes that trophic resources (ultimate factors) used by a population for raising young are predictable to varying degrees. Predictability (**Pr**) of the ultimate factor can be made up of two components: constancy (**C**) or contingency (**M**). The ratio, **M/C** (the **Ie** factor) is an indicator of the relative contributions of types of environmental information an individual within a population needs to regulate gonadal cycles and onset of breeding (Fig. 2).

For some populations, environmental conditions are highly constant and **Ie** is close to 0. In these cases it is possible that very little information is needed to regulate breeding. However, we feel that such cases are rare and in most other species and populations environmental signals are crucial for timing reproduction. The next question focuses on the extent to which populations in more seasonal environments use initial predictive versus supplementary cues. The relative contributions of these two types of information provide insight into the mechanisms by which an individual processes environmental signals into neuroendocrine and endocrine secretions. This theoretical relationship is summarized in Figure 2. If the **Ie** factor is <1 (**C** is high) then initial predictive cues, including external factors such as day length that either drives gonadal cycles or acts as a zeitgeber for endogenous rhythms (see Farner, '85; Gwinner, '87), may predominate. As the **Ie** factor increases to 1 (**C** and **M** have equal contributions) then more short-term and local cues (supplementary information) become important, but initial predictive information is still prevalent. When the **Ie** factor is >1 (**M** becomes greater than **C**), we suggest that both initial predictive and supplementary types of information are important and need to be integrated. As **Ie** increases further, the contribution of **M** becomes very high and supplementary information predominates over initial predictive cues. Thus, if the **Ie** factor can be calculated or even estimated, then through Figure 2 it is possible, in theory, to estimate the relative roles of initial predictive and supplementary information. Such theoretical estimates could then provide a firm base for elucidating mechanisms by which these individuals regulate and time breeding seasons. This format is testable, applicable to all vertebrates, and may provide a unifying hypothesis encompassing all the diverse breeding cycles known, and their proximate factors.

Given the increasing sensitivity to both initial predictive and supplementary types of information as **Ie** increases, the question then arises as to what mechanisms underly adjustments of gonadal maturation in response to these cues. Additionally, it is of interest how initial predictive and supplementary cues interact to time onset of breeding precisely. Many investigations have shown that photoperiod is an important environmental (initial predictive) factor regulating gonadal development (e.g., Farner, '85; Gwinner, '87). Furthermore, other investigations have probed the neuroendocrine mechanisms

underlying gonadal maturation (e.g., Follett, '84) and regression (photorefractoriness, e.g., Nicholls et al., '88). The subject continues to be active, but is not the main focus of this communication. Rather, we address the more neglected area of how supplementary cues influence reproductive function.

Low temperatures have been suggested to elevate plasma levels of thyroid hormones (thyroxine, T₄, and tri-iodothyronine, T₃) that in turn could influence gonadal maturation (e.g., Smith, '82). Alternatively, low or high temperature may activate the hypothalamo-adenohypophyseal-adrenocortical axis to increase secretion of circulating corticosterone (e.g., Holmes and Phillips, '76; Harvey et al., '84; Edens and Siegel, '75). Elevated secretory activity of adrenocortical tissue has also been shown to occur in response to food restriction (Holmes and Phillips, '76; Harvey et al., '84; Scanes et al., '80). Moreover, increased plasma levels of corticosterone are known to have the potential to suppress gonadal maturation at the hypothalamic (Wilson and Follett, '75), adenohypophyseal (Deviche et al., '79), or gonadal (Wingfield, '88) levels in birds. Corticosterone inhibition of gonadal development has been suggested as the mechanism by which drought retards breeding in bobwhite quail, *Colinus virginianus* (Cain and Lien, '85). Other, as yet unknown, mechanisms may be involved. Additional research in this area is clearly needed and comparisons of sedentary species that are likely to be most responsive to supplementary cues with migratory forms that are likely to be less responsive (e.g., sparrows of the genus *Zonotrichia* in Table 2) might be useful for identifying mechanisms.

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LITERATURE CITED

- Ashmole, N.P. (1963) The biology of the wideawake or sooty tern *Sterna fuscata* on Ascension Island. *Ibis*, 103b:297-364.
- Baker, J.R. (1938) The evolution of breeding seasons. In: Evolution. G.R. de Beer, ed. Oxford University Press, London, pp. 161-177.
- Balthazart, J. (1983) Hormonal correlates of behavior. In: Avian Biology. D.S. Farner, J.R. King, and K.C. Parkes, eds. Academic Press, New York, vol. 7, pp. 221-365.
- Berthold, P. (1988) The control of migration in European warblers. In: Acta XIX Congressus Internationalis Ornithologici. H. Ouellet, ed. University of Ottawa Press, Ottawa, pp. 215-250.
- Berthold, P., and E. Gwinner (1978) Jahresperiodik der Gonadengröße beim Fichtenkreuzschnabel (*Loxia curvirostris*). *J. Orn.*, 119:338-339.
- Blanchard, B.D., (1941) The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. Calif. Publ. Zool.*, 46:1-178.
- Blanchard, B.D., and M.M. Erickson (1949) The cycle in the Gambell Sparrow. *Univ. Calif. Publ. Zool.*, 47:255-318.
- Boag, P.T. and P.R. Grant (1984) Darwin's finches on Isla Daphne Major, Galápagos: breeding and feeding ecology in a climatically variable environment. *Ecol. Monogr.*, 54:463-489.
- Brown, L.H. and P.L. Britton (1980) The breeding seasons of East African birds. East Africa Natural History Society, Nairobi, 164 pp.
- Brown, N.L. and B.K. Follett (1975) Effects of androgen on the testis of intact and hypophysectomized Japanese quail. *Gen. Comp. Endocrinol.*, 33:267-277.
- Cain, J.R., and R.J. Lien (1985) A model for drought inhibition of bobwhite quail (*Colinus virginianus*). *Comp. Biochem. Physiol. [A]*, 82:925-930.
- Chapin, J.P. (1954) The calendar of wideawake fair. *Auk*, 71:1-15.
- Cohen, D. (1967) Optimizing reproduction in a varying environment. *J. Theor. Biol.*, 16:1-14.
- Colwell, R.K. (1974) Predictability, constancy, and contingency of periodic phenomena. *Ecology*, 55:1148-1153.
- Deviche, P., J. Balthazart, W. Heyns, and J.-C. Hendrick (1979) Inhibition of LH plasma levels by corticosterone administration in the male duckling (*Anas platyrhynchos*). *IRCS Med. Sci.*, 7:622.
- Edens, F.W., and H.S. Siegel (1975) Adrenal responses to high and low ACTH response lines of chickens during acute heat stress. *Gen. Comp. Endocrinol.*, 25:64-73.
- Engels, W.L., and C.E. Jenner (1956) The effect of temperature on testicular recrudescence in juncos at different photoperiods. *Biol. Bull.*, 110:129-137.
- Farner, D.S. (1970) Predictive functions in the control of annual cycles. *Environ. Res.*, 3:119-131.
- Farner, D.S. (1975) Photoperiodic controls in the secretion of gonadotropins in birds. *Am. Zool.*, 15:117-135.
- Farner, D.S. (1985) Annual rhythms. *Annu. Rev. Physiol.*, 47:65-82.
- Farner, D.S., and B.K. Follett (1979) Reproductive periodicity in birds. In: Hormones and Evolution. E.J.W. Barrington, ed. Academic Press, New York, pp. 829-872.
- Farner, D.S., and E. Gwinner (1980) Photoperiodicity, circannual and reproductive cycles. In: Avian Endocrinology. A. Epplé and M.H. Stetson, eds. Academic Press, New York, pp. 331-366.
- Farner, D.S., and R.A. Lewis (1971) Photoperiodism and reproductive cycles in birds. In: Photophysiology. A.C. Giese, ed. Academic Press, New York, vol. 6, pp. 325-370.
- Farner, D.S., and R.A. Lewis (1973) Field and experimental studies of the annual cycles of white-crowned sparrows. *J. Reprod. Fertil. [Suppl.]*, 19:35-50.
- Farner, D.S., and L.R. Mewaldt (1952) The relative roles of photoperiod and temperature in gonadal recrudescence in male *Zonotrichia leucophrys gambelii*. *Anat. Rec.*, 113:106.
- Farner, D.S., and D.L. Serventy (1960) The timing of reproduction in birds in the arid regions of Australia. *Anat. Rec.*, 137:354.

- Follett, B.K. (1984) Birds. In: Marshall's Physiology of Reproduction, Vol. 1. Reproductive Cycles of Vertebrates. G.E. Lamming, ed. Churchill Livingstone, Edinburgh, pp. 283–350.
- Fraser-Darling, F. (1938) Bird Flocks and the Breeding Cycle. Cambridge Univ. Press, Cambridge, 124 pp.
- Gibbs, H.L., and P.R. Grant (1987) Ecological consequences of an exceptionally strong El Niño event on Darwin's finches. *Ecology*, 68:1735–1746.
- Gwinner, E. (1987) *Circannual Rhythms*. Springer-Verlag, Berlin, 154 pp.
- Harding, C.F. (1981) Social modulation of circulating hormone levels in the male. *Am. Zool.*, 21:223–232.
- Harvey, S., J.G. Phillips, A. Rees, and T.R. Hall (1984) Stress and adrenal function. *J. Exp. Zool.*, 232:633–646.
- Holmes, W.N., and J.G. Phillips (1976) The adrenal cortex of birds. In: General, Comparative, and Clinical Endocrinology of the Adrenal Cortex. I. Chester-Jones, ed. Academic Press, New York, pp. 293–420.
- Immelmann, K. (1965) *Australian Finches*. Angus and Robertson, Sydney.
- Immelmann, K. (1971) Ecological aspects of periodic reproduction. In: *Avian Biology*. D.S. Farner and J.R. King, eds. Academic Press, New York, vol. 1, pp. 341–389.
- Immelmann, K. (1973) Role of the environment in reproduction as a source of predictive information. In: *Breeding Biology of Birds*. D.S. Farner, ed. Nat. Acad. Sci. USA, Washington, pp. 121–147.
- Jones, L.R. (1986) The effect of photoperiod and temperature on testicular growth in captive black-billed magpies. *Condor*, 88:91–93.
- Kendeigh, S.C. (1941) Length of day and energy requirements for gonad development and egg-laying in birds. *Ecology*, 22:237–246.
- King, J.R., B.K. Follett, D.S. Farner, and M.L. Morton (1966) Annual gonadal cycles and pituitary gonadotropins in *Zonotrichia leucophrys gambelii*. *Condor*, 68:476–487.
- Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen, London, 409 pp.
- Lehrman, D.S. (1965) Interaction between internal and external environments in the regulation of the reproductive cycle of the ring dove. In: *Sex and Behavior*. F. Beach, ed. Wiley, New York, pp. 355–380.
- Lewis, R.A., and D.S. Farner (1973) Temperature modulation of photoperiodically induced vernal phenomena in white-crowned sparrows (*Zonotrichia leucophrys*). *Condor*, 75:279–286.
- Ligon, J.D. (1971) Late summer-autumnal breeding of the Pinon jay in New Mexico. *Condor*, 73:147–153.
- Ligon, J.D. (1974) Green cones of the Pinon pine stimulate late summer breeding in Pinon jays. *Nature*, 250:80–83.
- Ligon, J.D. (1978) Reproductive interdependence of Pinon jays and Pinon pines. *Ecol. Monogr.*, 48:111–126.
- Lofts, B., and R.K. Murton (1968) Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J. Zool.*, 155:327–394.
- Lofts, B., R.K. Murton, and N.J. Westwood (1966) Gonadal cycles and the evolution of breeding seasons in British Columbidae. *J. Zool.*, 150:249–272.
- Marshall, A.J. (1959) Internal and environmental control of breeding. *Ibis*, 101:456–478.
- Marshall, A.J. (1970) Environmental factors other than light involved in the control of sexual cycles in birds and mammals. In: *La Photorégulation de la Reproduction Chez les Oiseaux et les Mammifères*. J. Benoit and I. Assenmacher, eds. Cent. Natl. Rech. Sci., Paris, pp. 53–64.
- Mewaldt, L.R., and J.R. King (1977) The annual cycle of white-crowned sparrows (*Zonotrichia leucophrys nuttallii*) in coastal California. *Condor*, 79:445–455.
- Miller, A.H. (1962) Bimodal occurrence of breeding in an equatorial sparrow. *Proc. Natl. Acad. Sci. U.S.A.* 48:396–400.
- Morton, E.S. (1971) Nest predation affecting the breeding season of the clay-colored robin, a tropical song bird. *Science*, 171:920–922.
- Murton, R.K., R.J.P. Thearle, and J. Thompson (1972) Ecological studies of the feral pigeon, *Columba livia*, var. 1. Population, breeding biology and methods of control. *J. Appl. Ecol.*, 9:835–874.
- Murton, R.K., and N.J. Westwood (1977) *Avian Breeding Cycles*. Oxford Univ. Press, London, 594 pp.
- Newton I. (1973) *Finches*. Taplinger, New York.
- Nicholls, T.J., A.R. Goldsmith, and A. Dawson (1988) Photorefractoriness in birds and comparison with mammals. *Physiol. Rev.*, 68:133–176.
- Payne, R.B. (1969) Breeding Seasons and the Reproductive Physiology of Tricolored Blackbirds and Red-Winged Blackbirds. Univ. Calif. Press, Berkeley.
- Perrins, C.M. (1970) The timing of bird breeding seasons. *Ibis*, 112:242–255.
- Rowan, W. (1925) Relation of light to bird migration and development changes. *Nature*, 115:494–495.
- Scanes, C.G., G.F. Merrill, R. Ford, P. Mauser, and C. Horowitz (1980) Effects of stress (hypoglycemia, endotoxin and ether) on the peripheral circulating concentration of corticosterone in the domestic fowl (*Gallus domesticus*). *Comp. Biochem. Physiol. [C]*, 66:183–186.
- Siegfried, W.R., and P.G.H. Frost (1975) Continuous breeding and associated behavior in the moorhen, *Gallinula chloropus*. *Ibis*, 117:102–109.
- Smith, J.P. (1982) Annual cycle of thyroid hormones in the plasma of white-crowned sparrows and house sparrows. *Condor*, 84:160–167.
- Sossinka, R. (1980) Ovarian development in an opportunistic breeder, the zebra finch, *Poephila guttata castanotis*. *J. Exp. Zool.*, 211:225–230.
- Storey, C.R., and T.J. Nicholls (1982) Low environmental temperature delays photoperiodic induction of avian testicular maturation and the onset of postnuptial refractoriness. *Ibis*, 124:172–174.
- Suomalainen, H. (1937) The effect of temperature on the sexual activity of non-migratory birds stimulated by artificial lighting. *Ornis Fenn.*, 14:108–112.
- Tordoff, H.B., and W.R. Dawson (1965) The influence of day light on reproductive timing in the red crossbill. *Condor*, 67:416–422.
- Vleck, C.M., and J. Friedkalns (1985) Reproduction in zebra finches: hormone levels and effect of dehydration. *Condor*, 87:37–46.
- Wilson, F.E., and B.K. Follett (1975) Corticosterone-induced gonadosuppression in photostimulated tree sparrows. *Life Sci.*, 17:1451–1456.
- Wingfield, J.C. (1980) Fine temporal adjustment of reproductive functions. In: *Avian Endocrinology*. A. Eppe and M.H. Stetson, eds. Academic Press, New York, pp. 367–389.
- Wingfield, J.C. (1983) Environmental and endocrine control of reproduction: an ecological approach In: *Avian Endocrinology: Environmental and Ecological Aspects*. (S.-I. Mikami, and M. Wada eds. Jap. Sci. Soc. Press, Tokyo, and Springer-Verlag, Berlin, pp. 149–166.
- Wingfield, J.C. (1988) Changes in reproductive function of free-living birds in direct response to environmental perturbations. In: *Processing of Environmental Information in Vertebrates*. M.H. Stetson, ed. Springer-Verlag, Berlin, pp. 121–148.

- Wingfield, J.C., G.F. Ball, A.M. Dufty, Jr., R.E. Hegner, and M. Ramenofsky (1987) Testosterone and aggression in birds: tests of the challenge hypothesis. *Am. Sci.*, 75:602–608.
- Wingfield, J.C., and D.S. Farner (1978) The annual cycle in plasma irLH and steroid hormones in feral populations of the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *Biol. Reprod.*, 19:1046–1056.
- Wingfield, J.C., and D.S. Farner (1980) Environmental and endocrine control of seasonal reproduction in temperate zone birds. *Prog. Reprod. Biol.*, 5:62–101.
- Wingfield, J.C., and G.J. Kenagy (1991) Natural control of reproduction. In: *Handbook of Comparative Endocrinology*. P.K.T. Pang and M.P. Schreibman, eds. Academic Press, New York, vol. 4, pp. 181–241.
- Wingfield, J.C., and P. Marler (1988) Endocrine basis of communication: reproduction and aggression. In: *The Physiology of Reproduction*. E. Knobil and J.D. Neill, eds. Raven Press, New York, pp. 1647–1677.
- Wingfield, J.C., and M.C. Moore (1987) Hormonal, social and environmental factors in the reproductive biology of free-living male birds. In: *Psychobiology of Reproductive Behavior*. D. Crews, ed. Prentice Hall, Englewood Cliffs, New Jersey, pp. 149–175.
- Wingfield, J.C., J.P. Smith, and D.S. Farner (1982) Endocrine responses of white-crowned sparrows to environmental stress. *Condor*, 84:399–409.
- Witschi, E. (1961) Sex and secondary sex characters. In: *Biology and Comparative Physiology of Birds*. A.J. Marshall, ed. Academic Press, New York, vol. 2, pp. 115–168.