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Review article

Individual variation and the challenge hypothesis

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A B S T R A C T

In this paper I discuss how the challenge hypothesis (Wingfield et al., 1990) influenced the development of ideas about animal personality, and describe particularly promising areas for future study at the intersection of these two topics. I argue that the challenge hypothesis influenced the study of animal personality in at least three specific ways. First, the challenge hypothesis drew attention to the ways in which the environment experienced by an organism – including the social environment – can influence biological processes internal to the organism, e.g. changes to physiology, gene expression, neuroendocrine state and epigenetic modifications. That is, the challenge hypothesis illustrated the bidirectional, dynamic relationship between hormones and (social) environments, thereby helping us to understand how behavioral variation among individuals can emerge over time. Because the paper was inspired by data collected on free living animals in natural populations, it drew behavioral ecologists' attention to this phenomenon. Second, the challenge hypothesis highlighted what became a paradigmatic example of a hormonal mechanism for a behavioral spillover, i.e. testosterone's pleiotropic effects on both territorial aggression and parental care causes aggression to “spillover” to influence parenting behavior, thereby limiting behavioral plasticity. Third, the challenge hypothesis contributed to what is now a cottage industry examining individual differences in hormone titres and their relationship with behavioral variation. I argue that one particularly promising future research direction in this area is to consider the active role of behavior and behavioral types in eliciting social interactions, including territorial challenges.

1. The challenge hypothesis brought behavioral ecologists' attention to the ways the social environments can get “under the skin”

According to the challenge hypothesis, the endocrine system responds to social interactions. Specifically, Wingfield et al. (1990) hypothesized that testosterone transiently increases in response to a territorial challenge in male birds. Rather than viewing hormones as deterministic causes of phenotypes, the challenge hypothesis drew attention to the ways in which the environment can change physiology, and to potentially influence future behavior: not only do androgens facilitate the development of sexual ornaments, which influences the way that a male behaves and is treated by his social group, but androgens also change in response to social interactions, and in response to changes in ornaments, e.g. plumage coloration (Rubenstein and Hauber, 2008; Safran et al., 2008). This insight influenced what is now a burgeoning literature on individual variation because it contributed to our understanding of the ways in which phenotypes are constructed, which is a central question in the study of animal personalities, i.e. the study of individual differences in behavior that are maintained over time and/or across contexts.

While laboratory studies in model organisms had started to reveal the ways in which environments (including the social environment) influence endocrine state for decades prior to the publication of Wingfield et al. (1990), e.g. (Lehrman, 1964), the bidirectional

relationship between hormones and behavior was not featuring prominently in the behavioral ecology literature when the challenge hypothesis was published in 1990. But the challenge hypothesis caught the attention of behavioral ecologists because: 1) it was inspired by data that were collected on free-living animals in natural populations, rather than model organisms in the lab; 2) it generated a hypothesis relevant to what was at the time a very popular topic in behavioral ecology (mating systems); 3) it argued that the endocrine system is responsive to social cues, not to just physical cues such as day length and temperature. The idea that brief social interactions can provoke neuroendocrine changes opened up the possibility that hormonal mechanisms might be relevant to all sorts of social behaviors that operate over relatively short time periods – hormones do not just change slowly in accordance with seasonal changes, for example, but also exhibit transient changes in response to even brief social cues, such as a territorial intrusion, or a mating opportunity. This line of thinking contributed to the appreciation that hormones can act as integrators of information about subtle changes in the environment, including the social environment; environmental cues trigger changes in neuroendocrine state, which can go on to influence future phenotypes (Fig. 1). Whether and how those responses internal to the animal are involved with coping with the immediate challenge and/or preparing for future ones is still an open question.

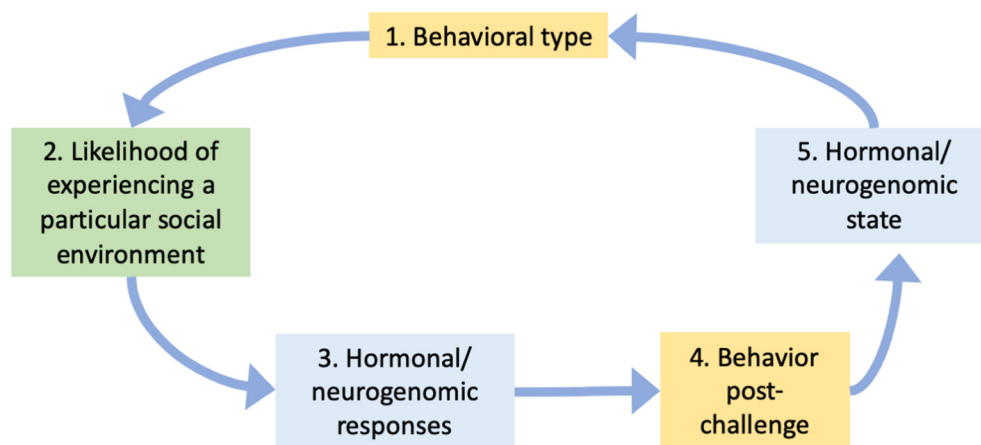
These ideas are highly relevant to animal personality because appreciating the dynamic back-and-forth between environments and

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behavior, and behavior can influence the environments experienced, thereby illustrating the two-way relationship between environments and physiology (processes under the skin), with the behavior of the organism at the interface. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

processes internal to the animal helps us to understand how phenotypes are constructed, and why they differ among individuals. That is, within the animal personality literature, we would like to know how environments interact with proximate physiological, molecular, and genomic mechanisms to shape individual behavioral variation. By showing that the social environment influences neuroendocrine state relevant to social behaviors, the challenge hypothesis contributed to the appreciation that the relationship between hormones and behavior is not just a one-way interaction but is instead bidirectional. This message – that hormones and other gene products are not always causal or deterministic but instead lie at the interface between phenotypes and environments – is a key message from the last 30+ years of studies of mechanisms of behavioral development that has still not yet fully penetrated the social and behavioral sciences.

More recently, the idea that environments can get under the skin is gaining foothold in part because of renewed interest in epigenetic mechanisms, and growing recognition that the genome – like the endocrine system – is also socially and environmentally responsive, even to transient social stimuli. For example, genome-wide transcription studies have revealed that roughly ~10% of the genome responds to a *mating opportunity* (Bloch et al., 2018; Carney, 2007; Cummings et al., 2008; Fraser et al., 2014; Lawnczak and Begun, 2004; Mack et al., 2006; McGraw et al., 2008), *predation risk* (Jansen et al., 2013; Lavergne et al., 2014; Sanogo et al., 2011), or a *territorial challenge* (Alaux et al., 2009; Bukhari et al., 2017; Rittschof et al., 2014; Rittschof and Robinson, 2013; Sanogo et al., 2012). Hormones have important roles to play in the broader discussion about how environments get under the skin at the molecular level because hormones are not only gene products, but they can themselves influence the expression of other genes, which puts them at the center of the effort to bridge the gap between genes and social behavior (Adkins-Regan, 2004).

2. The challenge hypothesis drew attention to what became a paradigmatic example of a hormonal mechanism causing a behavioral spillover

The key ingredients to animal personality are that a) individuals behave differently from one another; b) individuals have a behavioral type that they retain through time and across situations. One of the reasons that animal personality started attracting attention in the mid-2000s was that Sih et al. (2004a, 2004b) pointed out that within-individual consistency could reflect limited behavioral plasticity. That is, when individuals have a behavioral type that is somewhat stable over time or across situations, this could result in “behavioral spillovers” and limited plasticity, e.g. a bold individual could be inappropriately bold

in the wrong situations. Recognition of the potential maladaptive consequences of personality inspired new theory about the adaptive causes of personality variation (Dall et al., 2004; Dingemans and Réale, 2005; Dingemans and Wolf, 2010), and contributed to the popularity of the topic.

One of the ways in which the challenge hypothesis has influenced the study and understanding of animal personality is that it provided what is now a paradigmatic example of a behavioral spillover, thereby bolstering the claim that limited plasticity can result from a proximate constraint. That is, one interpretation of the challenge hypothesis is that interspecific variation in circulating androgens reflects a tradeoff between territorial aggression and paternal care. The general idea was that aggression and paternal care might be negatively associated within individual males because they can’t “turn off” a generally aggressive tendency caused by high circulating concentrations of testosterone, for example. This idea stemmed from one of the findings by Wingfield et al. (1990): “monogamous” male territorial birds – in which both parents typically provide care for the offspring – are more hormonally responsive (in terms of the difference between baseline and peak testosterone) than polygynous male territorial birds (Fig. 7 in Wingfield et al., 1990). Monogamous birds produce high levels of androgens following a territorial intrusion, but otherwise have relatively low circulating androgens. The interpretation was that monogamous males have a more transient hormonal response to a territorial challenge response because androgens have inhibitory effects on paternal care. Polygynous birds, on the other hand, can “afford” to have constitutively high levels of androgens because they do not typically provide paternal care. In other words, androgens could mediate the tradeoff between territorial aggression and paternal care because aggression-induced testosterone could “spill over” into parental care.

In some species, androgens do appear to have inhibitory effects on paternal care. For example, short term peaks of testosterone suppress paternal care in redstarts (Goymann and Flores Davila, 2017), and testosterone-implanted male juncos provide less parental care (Ketterson and Nolan, 1999). However, overall evidence for the idea that androgens inhibit paternal care has been mixed (reviewed in Hirschenhauser and Oliveira, 2006). Regardless, the importance of the challenge hypothesis is not that it was necessarily “right”, but it influenced the way we study and think about hormones and behavior.

A legacy of Wingfield et al. (1990) for the study of animal personality is that it gave some plausibility to the suggestion that a mechanistic constraint could limit an individual's behavioral type. The idea that hormones might act as a mechanistic constraint or mediator of behavioral tradeoffs was highly influential in the development of ideas about behavioral syndromes, i.e. among individual behavioral

correlations, because part of what originally motivated interest in behavioral syndromes was that an individual's behavior might be constrained by their neuroendocrine system or another proximate constraint.

More generally, there has been interest in the idea that an individual's behavioral type is set by a slower-changing “state” variable such as metabolic rate (Mathot et al., 2018) or neuroendocrine state (Sih et al., 2015), and that might help explain within-individual consistency in behavior. If an individual's behavioral type is anchored by their neuroendocrine system, then we would expect hormones to change relatively slowly over time compared to behavior. Recent meta-analyses showing that the repeatability of circulating steroids is equal to or less than repeatability of behavior in birds (Fanson and Biro, 2019; Holtmann et al., 2017) is not consistent with this hypothesis, but whether circulating hormones are really the best way to characterize an individual's behavioral type (as opposed to, for example, receptor densities or neuroanatomical differences) is debated (Ball and Balthazart, 2008).

A promising area for future work is to examine endocrine mediators of within-individual tradeoffs across contexts or situations (behavioral syndromes), rather than endocrine mediators of within-individual behavioral consistency through time. Despite the attention the idea received in Sih et al. (2004a, 2004b), the idea that hormonal pleiotropy contributes to behavioral correlations across contexts or situations is still relatively unexplored, especially in an ecological context. That is, despite the initial suggestion (inspired, in part, by the challenge hypothesis), that hormones are a plausible mechanism that can cause behavioral spillovers/limited behavioral plasticity and that hormonally-mediated tradeoffs have an important role in structuring life history variation (Lessells, 2008), hormonally-mediated tradeoffs in the context of animal personality are still relatively unexplored, even though they are still quite compelling.

While testosterone as the key mediator of the tradeoff between aggression and parental care is debatable, there are many other hormones – and not just sex steroids – that are highly pleiotropic, thereby potentially causing different behaviors to covary together. Moreover, the social behavior network in the brain of vertebrates – thought to be involved in processing and responding to various types of social information (e.g. mating, courtship, aggression, parental care) – contains nodes for many steroid receptors (Cardoso et al., 2015; Goodson, 2005; Newman, 1999; O'Connell and Hofmann, 2011), thereby providing a central mechanism that can proximately link behaviors in different contexts together in the brain. Particularly promising mechanisms hormonal include the melanocortin system (Ducrest et al., 2008), juvenile hormone in insects (Flatt et al., 2005; Fry, 2006; Schwenke et al., 2016), serotonin and the gut-brain axis (Bellono et al., 2017; Cryan and Dinan, 2012) and the link between feeding and social behavior, e.g. NPY (Heilig, 2004) and galanin (reviewed in Fischer and O'Connell, 2017).

3. The challenge hypothesis contributed to what is now a cottage industry examining individual differences in hormone titres

In their original paper, Wingfield et al. (1990) showed that there was variation among species in hormonal responsiveness to a territorial challenge, and they put forward the hypothesis that variation in androgen responsiveness was related to mating systems. In other words, they suggested that variation among species in hormonal responsiveness is biologically meaningful rather than just noise. A major insight of this hypothesis, then, is that animals respond hormonally to challenges in their environment (including social challenges) and that the magnitude of this response varies. An obvious question, then, is whether variation *among individuals within species* in hormonal responsiveness also has adaptive significance. That is, can the same hypothesis (i.e. the challenge hypothesis) that attempts to explain variation *among species* also explain variation *within species*: do more monogamous/caring

males exhibit a more transient testosterone response to a challenge than more promiscuous/noncaring males? Since Wingfield et al.'s classic study, coincident with growing appreciation for individual variation in many aspects of biology, behavioral endocrinologists have been increasingly interested in endocrine variation among individuals within species, and how endocrine variation covaries with behavioral variation at the individual level.

The literature on individual differences in hormone signaling is well reviewed elsewhere (Kempnaers et al., 2008; Williams, 2008), with several important insights, e.g. the importance of characterizing individual reaction norms, difficulties with interpreting hormone-behavior correlations, etc. (Taff and Vitousek, 2016). But in general, there are three types of questions that are currently actively being pursued: 1) Are rank order differences in circulating hormone titres among individuals consistent over time? 2) Is continuous variation in behavior correlated with circulating hormones among individuals at a given point in time? 3) Do behavioral types differ in the *responsiveness* of their endocrine system?

3.1. Are rank order differences in circulating hormone titres among individuals consistent over time?

Repeatability measures the extent to which variation among individuals is consistent across measurements. Recent meta-analyses of the repeatability estimates of circulating steroids (glucocorticoids and sex steroids) have suggested that repeatability decreases as the interval between measurements increases (Fanson and Biro, 2019), that acute/induced hormone titres (especially glucocorticoids) are more repeatable than baseline hormone titres (Fanson and Biro, 2019; Holtmann et al., 2017), and that variation in hormone titres tend to be less repeatable than metabolism or behavioral traits (Holtmann et al., 2017), perhaps because there is more error associated with their measurement (detection limits, assay variation), or because hormones are highly responsive to external factors. For meta-analyses of the repeatability of glucocorticoids in particular see Schoenemann and Bonier (2018) and Taff et al. (2018). There is also interest in generating statistical methods to quantify the repeatability of measurements within individuals, i.e. profile repeatability (Reed et al., 2019). Finally, several authors have suggested that individual differences are more likely to be observed at the receptor level (density or affinity) or neuroanatomically, and have pointed out that few studies have characterized variation in binding globulin action or intracellular signaling pathways (Ball and Balthazart, 2008; Williams, 2008).

3.2. Is behavioral variation correlated with circulating hormones among individuals at a given point in time?

There has been interest in measuring the association between circulating hormone titres and behavioral variation among individuals because if hormone titres are correlated with behavior at the individual level (e.g. van Oers et al., 2011), then this could provide support for the idea that behavioral types reflect differences in endocrine state. However, the jury is still out on this point, in part because there is some skepticism about how to interpret patterns (or lack of) of covariations between hormones and behavior at the individual level (Ball and Balthazart, 2008; Hau and Goymann, 2015; Hews and Moore, 1997). This is because there are mechanistic reasons to suspect that hormones influence behavior in a probabilistic manner, mediated by hormonal threshold functions. Therefore the relationship between and hormones is likely to be nonlinear and difficult to detect with statistical methods that assume additive, linear relationships (Goymann and Flores Davila, 2017).

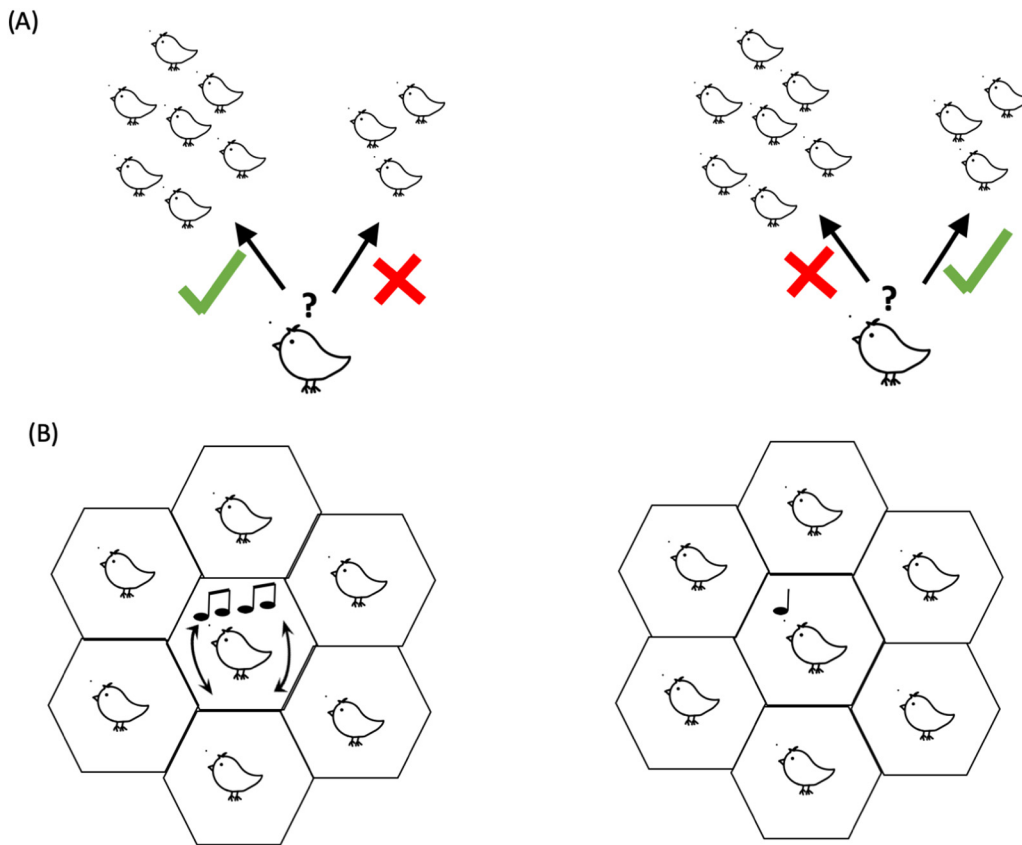


Fig. 2. Two ways in which individuals might differ in the likelihood of experiencing territorial intrusions. A) Individuals differ in social group size preference, i.e. whether they prefer to occur in relatively small or large groups (indicated by green checks or red x's), which could influence encounter rates with neighbors or intruders; B) some behavioral types of individuals (left) are more likely to encounter neighbors or intruders than other behavioral types (right) because, for example, they patrol their territories (indicated by double arrows) or sing more. Hexagons indicate territorial boundaries. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Do behavioral types differ in the responsiveness of their endocrine system?

Another reason for the failure to detect hormone-behavior correlations is that a single snapshot of circulating hormones might be insufficient to assess an individual's endocrine type. Because the endocrine system is inherently flexible, some authors have suggested that an individual's endocrine type is better measured by hormonal responsiveness, which is more likely to be correlated with personality traits (Taff and Vitousek, 2016). This idea was actually strongly emphasized in the original coping styles literature, which argued that proactive and reactive individuals differ in the reactivity of the hypothalamic-pituitary-adrenal (HPA) and activity of the hypothalamic-pituitary-gonadal (HPG) axis (Koolhaas et al., 1999).

There is some support for the hypothesis that there is interesting, biologically meaningful variation among individuals in their endocrine type, and in the context of androgen responsiveness, authors have taken one of two approaches to assess the responsiveness of the HPG axis in order to determine whether some individuals are more hormonally responsive than others: 1) reaction norm approach; 2) gonadotropin releasing hormone (GnRH) challenge.

3.3.1. Reaction norm approach

Instead of simply capturing a snapshot of steroids in circulation at a given point in time and trying to relate them to individual behavior, another approach is to characterize individuals' hormonal reaction norms by measuring circulating androgens pre- versus post-challenge. This approach is appealing for many reasons (reviewed in Hau and Goymann, 2015), and the development of noninvasive methods (fecal, urine, etc.) has assisted with this effort, both because it allows collection on smaller organisms where repeated blood sampling is not feasible, and it avoids problems introduced by repeated handling to collect blood. However, an important caveat is that non-blood measures are not always reflective of the hormones in circulation that are available to

receptors. Another challenge with the reaction norm approach (whether on blood or a proxy) is that accurately characterizing individual variation in reaction norms requires large amounts of statistical power (Martin et al., 2011), which might be beyond the scope of many studies.

3.3.2. GnRH challenge

Another way to characterize the responsiveness of the HPG axis is to “challenge” the system by injecting GnRH, a pituitary hormone which stimulates the testes to produce testosterone. An increase in testosterone in response to GnRH reflects an individual's capacity to produce testosterone: the testes can't produce more testosterone than maximal stimulation with GnRH can induce them to (Goymann and Davila, 2017). Some of the best examples of the success of this method are illustrated by studies in juncos (Jawor et al., 2006), e.g. GnRH-induced testosterone predicts individual variation in male aggression and other phenotypes (McGlothlin et al., 2008; McGlothlin et al., 2007), among-male variation in response to GnRH challenge is correlated with reproductive success in a natural population (McGlothlin et al., 2010, see also Bergeon Burns et al., 2014). For examples in other birds see Ambardar and Grindstaff (2017) and Goymann et al. (2015).

4. Future directions

Moving forward, a particularly promising area for future study at the interface of the challenge hypothesis and animal personality has to do with the active role of behavior and behavioral types in experiencing territorial challenges.

We typically study the challenge hypothesis by staging territorial intrusions, and we often observe variation among individuals in the ways that they respond to a staged territorial intrusion at both the behavioral and hormonal level. However, consideration of individual differences prompts a different perspective, i.e. that some behavioral types of individuals might be more likely than others to experience territorial challenges in the first place. From this perspective, behavior

plays an active role in how animals experience different environments (including social environments) (Bateson, 1988), and therefore the frequency with which they elicit social interactions.

There are at least two plausible mechanisms that could cause some individuals to be more likely to experience social challenges (territorial intrusions) than others (Fig. 1). First, even after controlling for differences in habitat quality, individuals might differ in group size preference, such that some individuals, e.g. highly social ones, end up settling in high density areas – where they are more likely to experience territorial challenges – compared to individuals that settle in low density areas (Fig. 2a). Indeed, there is some evidence for consistent, heritable differences among individuals in social group size use. Individual swallows, for example, made different choices about colony size (Brown and Brown, 2000), and some individual *Drosophila* preferred to associate with larger groups while other individuals prefer to associate with smaller groups (Saltz, 2011). Second, some behavioral types of individuals might be generally more aggressive or primed to provoke intrusions, e.g. they spend more time patrolling their territory looking for intruders or call more compared to other territory holders which elicit fewer challenges from their neighbors or floaters (Fig. 2b).

When behavioral types assort nonrandomly into different habitats, or experience different social environments generally, e.g. (Saltz, 2011), then their behavioral type could cause them to experience a particular social environment, which in turn causes a particular regimen of activation of the neuroendocrine system. In other words, this is an example of behavioral types driving the activation of the endocrine system, rather than the other way around. It will be fascinating for future studies to begin to connect the dots between behavioral type-dependent social environment use, endocrine activity in response to territorial challenges, and to understand how hormones feedback to influence future behavior and the subsequent activity of the endocrine system (Fig. 1).

5. Concluding remarks

One of the lasting legacies, I think, of the challenge hypothesis is that it made hormones relevant to ecologists. Capitalizing on what was at the time relatively new technology that allowed field researchers to measure circulating hormones in blood (radioimmunoassay), Wingfield et al. (1990) showed that hypotheses about hormones don't have to rely on invasive, surgical (i.e. gland removal) methods, or be confined to model organisms in the lab. Therefore, the challenge hypothesis paved the way for more integrative studies of behavior generally; this line of work opened up new research areas about the ecology and evolution of hormonal mechanisms, and helped to move the new discipline of field endocrinology forward. Along the way, it contributed to the development of ideas about animal personality, inspiring us to look more closely at the proximate mechanisms that can cause behavioral types and behavioral variation.

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