Positive Feedback between Behavioral and Hormonal Dynamics Leads to Differentiation of Life-History Tactics

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ABSTRACT: Competitive interaction among individuals of a single population may result in the differentiation of two or more distinct life-history tactics. For example, although they exhibit unimodal size distribution, male juveniles of salmonids differentiate into those going down to the ocean to grow and returning to the natal stream after several years to reproduce (migratory tactic) and those staying in the stream and reproducing for multiple years (resident tactic). In this study, we developed a simple mathematical model for the positive feedback between hormonal and behavioral dynamics, with the expectation of establishing multiple discrete clusters of hormone levels leading to differentiation of life-history tactics. The assumptions were that probability of winning in fighting depends both on the body size and hormone level of the two contestants. An individual with a higher hormone level would be more likely to win the competition, which further enhanced hormone production, forming a positive feedback loop between hormone level and fighting ability. If the positive feedback was strong but not excessive, discrete clusters of hormone levels emerged from a continuous distribution. In contrast, no clear clustering structure appeared in the distribution of hormone levels if the probability of winning in fighting was controlled by the body size.

Keywords: alternative life-history tactics, decision-making, behavioral and hormonal feedback, individual-based model, dominance hierarchy.

Introduction

Alternative life-history tactics comprise discontinuous patterns of phenotypic variation arising from the continuous status, realized by divergent developmental programs (Roff 1996). For example, in scarab beetles, large males develop horns and behave as fighters, whereas the others become sneakers (Emlen 1997). Some coral fish change their sex on the basis of body size and social rank (Fricke and Fricke 1977; Warner and Robertson 1978; Kuwamura and Nakashima 1998; Munday et al. 2006). Generally, individuals choose a tactic at a particular time in their life on the basis of a given environment and/or their status in the population.

Salmonid fish exhibit extreme alternative life-history tactics. Some individuals migrate to the ocean to feed, grow to a much larger size, and return to the natal stream for reproduction (migratory tactic), whereas others mature early and complete their entire life cycle in freshwater streams (resident tactic; Morita and Nagasawa 2010; Morita et al. 2014). Larger male juveniles tend to choose the resident tactic, which is common throughout salmonids (Aubin-Horth and Dodson 2004; Piché et al. 2008). This trend can be explained by the competition among these fish, as residents suffer from intensive competition for both spawning and feeding opportunities, resulting in a dominance hierarchy among residents (Nakano 1995; Esteve 2011). Consequently, the reproductive success of an individual adopting the resident tactic strongly correlates with their body size in the juvenile state, because they mature at younger ages without experiencing a feeding migration (Morita et al. 2014).

Alternative behaviors or morphological types represent the output of complex physiological pathways controlled by gene expression (Oliveira 2009). In salmonids, several factors, including growth and stress, have been proposed to mediate seaward migrating behavior (Clements and Schreck 2004; Ojima and Iwata 2010). However, how these physiological factors relate to the development of alternative tactics and how body size contributes to it are still unclear.

In modeling salmonid population dynamics, the life-history decision of male juveniles has been assumed to follow a threshold rule (Tachiki and Koizumi 2016; Horita
et al. 2018), in which the individuals remain in the stream if their body size (or a status parameter) is larger than a threshold; otherwise, they migrate to the ocean. However, although the mean body size of juveniles adopting the resident tactic is larger than that of migratory juveniles, the actual body size distribution exhibits a single peak without a clear separation of two groups of individuals (Morita and Nagasawa 2010). This implies that an endocrine system drives different developmental pathways depending on the status of each individual, even if the body size is similar among individuals. The purpose of this study is to propose a system that could explain the induction of discrete patterns of physiological states serving to establish the threshold assumed by prior studies.

We conjectured that the level of a key hormone changes in response to competitive interaction with other individuals, and that the resultant distribution of the hormone levels exhibits two or more clusters, leading to the distinct developmental fates. For salmonids, one candidate for the key hormone in juvenile males’ life-history choice is 11-ketotestosterone (11-KT), as in many animals, maturation is induced by sex steroids (Devlin and Nagahama 2002). In salmonids, 11-KT functions as an androgen, whereas estradiol-17β (E2) serves as the estrogen. These hormones contain a steroid nucleus and are synthesized from testosterone. Moreover, in masu salmon, the plasma level of 11-KT and testosterone of mature males is higher than that of immature males, and the migration of individuals can be suppressed when 11-KT and testosterone are artificially injected (Munakata 2012).

The production of steroid hormones is induced by several biotic factors (e.g., competition; Perry and Grober 2003) and abiotic factors (e.g., water quality; Awata et al. 2011), which may vary among seasons (Munakata et al. 2001; Munakata 2012). Social interaction is one of the most important stimuli that affect hormone production (Perry and Grober 2003; Lorenzi and Grober 2012). The results of competitive interaction affect the production of sex steroid hormone, modify the behavior of the individual, and change the results of future competition (Wingfield and Wada 1989). For example, the plasma level of androgen significantly differs between the winner and loser in Neolamprologus pulcher (Taves et al. 2009). Because androgen enhances activity and renders behavior more aggressive (Hirschhausen and Oliveira 2006; Taves et al. 2009; Nelson and Kriegsfeld 2016), an individual who wins a competition becomes more likely to win the next competition, which is termed the winner-loser effect (Earley et al. 2013; Li et al. 2014). Salmonid fish compete over food resources and space in streams, forming a dominance hierarchy (Nakano 1995). The social interaction may thus affect the life-history choice of an individual through differentiation of the endocrine level.

In this study, we constructed a mathematical model for the hormonal dynamics that are coupled with individual growth and competitive interactions and investigated how the distribution of hormone levels in the population changed depending on the physiological and ecological processes (fig. 1). We demonstrated that the distribution of hormone level formed multiple clusters when the hormone level largely contributes to the probability of winning. Our study shows that ecological interactions such as competition can give rise to discrete phenotypes for diverse traits such as life-history tactics via hormonal dynamics without assuming the presence of a threshold.

Material and Methods

Life Histories and Sex Steroids of Salmonids

We considered a mathematical model for competitive interaction among juveniles and analyzed the resultant patterns of individual growth and hormone level. In this study, we focused on masu salmon (Onchorhynchus masou masou) because they exhibit a typical and relatively simple life history of salmonids. Some males complete their entire life cycle in freshwater streams (residents), whereas others migrate to the ocean (migrants).

Among factors previously proposed to determine life-history choice, the concentration of key hormones, lipid storage, and growth efficiency have been shown to affect the propensity to realize alternative phenotypes (Dodson et al. 2013). We here considered the situation in which the proximal factor of the decision-making is endocrine status (i.e., hormone level), and the correlation between decision-making and body size results from the correlation between hormone level and body size. Empirical evidence suggests that a sexual hormone constitutes a key factor for life-history choice in masu salmon. As Munakata (2012) measured the time series of plasma androgen levels of 0+ males and showed that the plasma levels of testosterone and 11-KT in mature males were significantly higher than those in nonmature males, in the present study we considered testosterone as a factor inducing maturation.

Androgen production is induced by both biotic and abiotic factors. Here, we focused on social interaction, especially competition that stimulates hormone production (Perry and Grober 2003; Lorenzi and Grober 2012). We also considered that the steroid hormone changes the behavior of the individual and modifies the result of future competition. In particular, an individual retaining a higher hormone concentration is likely to win a competition (Taves et al. 2009).

Scheme of Individual-Based Simulation

In the model, we considered a population consisting of N = 100 juveniles. The body size and hormone level
of individual $i$ ($i = 1, 2, \ldots, N$) at time $t$ were denoted by $s_i$ and $h_i$, respectively. The initial body size and hormone level of each individual was a stochastic variable following a bivariate normal distribution. We assumed that the growth rate and hormone plasma level were affected by the outcomes of fighting with other individuals.

We traced the dynamics of hormone level and body size of each individual in terms of a continuous-time stochastic individual-based model (Gillespie 1977). A single time step in the simulation model consisted of the three processes that follow:

Process 1. The time lapse $\Delta t$ until the next event is drawn from an exponential distribution with mean $1/E$, where $E$ represents the event rate and is defined as follows:

$$E = qN(N - 1),$$  \hspace{1cm} (1)

where $q$ is a rate constant for an individual to encounter with an opponent. When $E$ is larger, fighting events occur more frequently.

Process 2. Two individuals are randomly chosen from the population. These individuals fight each other, with one declared as the winner. The probability that individual $i$ wins the fight against individual $j$ is denoted by $\varepsilon_{ij}$. We assume that $\varepsilon_{ij}$ is given as

$$\varepsilon_{ij} = \frac{1}{1 + (s_j/s_i)^{\lambda_s}(h_j/h_i)^{\lambda_h}}. \hspace{1cm} (2)$$

Note that $\varepsilon_{ij} = 1 - \varepsilon_{ij}$ is satisfied. Also note that the probability of winning of $i$ against $j$ is an increasing function of the ratio of $(s_j/s_i)^{\lambda_s}(h_j/h_i)^{\lambda_h}$ to $(s_j/s_i)(h_j/h_i)$

Hence, the probability of winning depends both on the relative body size and the relative hormone level. The weighting factor for the body size is $\lambda_s$ and that for the hormone level is $\lambda_h$. Suffixes $s$ and $h$ represent size and hormone, respectively. $\lambda$ indicates the sensitivity of each element to the probability of winning. When $\lambda_s$ ($\lambda_h$) is large, a slight difference in size (hormone level) between individuals becomes a large difference in the probability of winning. $\lambda$ is larger if an organism is capable of recognizing their relative competitive ability more accurately. As $s_i$ (or $h_i$) increases, $\varepsilon_{ij}$ increases and finally converges to 1. If both $s_i = s$ and $h_i = h$ are satisfied, the two contestants have an equal chance of winning: $\varepsilon_{ij} = 0.5$.

Process 3. Winners can obtain more resources, resulting in a faster growth rate than that of losers. In addition, winners synthesize testosterone and enhance the hormone

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{model_scheme}
\caption{Scheme of the model. All individuals hatch in the river and decide whether to stay in the river or migrate to the sea. Juveniles compete with each other, and the winners synthesize more androgen than the losers. Winners become more likely to win in subsequent competitive events because androgen enhances aggressiveness, resulting in two distinct types of juveniles that differ markedly in androgen level. Because androgen also induces maturation, those juveniles with high androgen levels become residents, and those with low androgen levels migrate to the sea.}
\end{figure}
level. Size growth dynamics are modeled according to the von Bertalanffy model of the first order, which is commonly used in fishery sciences for describing the growth of body length (rather than body weight; von Bertalanffy 1938; Kiso et al. 1992; Snover et al. 2005). We assume that the hormone is synthesized at a constant rate and is decomposed in proportion to the current level. If individual i wins the competition, the body size and hormone level of the individual change until the next fighting event according to the equations that follow:

$$\frac{ds_i}{dt} = \alpha_s (1 + \gamma) - \beta_s s_i,$$

(3a)

$$\frac{dh_i}{dt} = \alpha_h - \beta_h h_i.$$

(3b)

In contrast, if individual i loses, the body size and hormone level of the individual change with the equations that follow:

$$\frac{ds_i}{dt} = \alpha_s - \beta_s s_i,$$

(4a)

$$\frac{dh_i}{dt} = -\beta_h h_i.$$

(4b)

In equations (3) and (4), \(\alpha_s\) and \(\gamma\) are coefficients of anabolism and \(\beta_s\) is a coefficient of catabolism (von Bertalanffy 1938). The rate of hormone synthesis is \(\alpha_h\), and the rate of degradation is \(\beta_h\). The winner increases with regard to both size and hormone level, rendering the individual more likely to win in subsequent encounters. The body sizes and hormone levels of all individuals are updated until the next fighting event. We assume that the rate of hormonal change is much faster than that of size growth (Lindstedt et al. 1992; Snover et al. 2005). We assume that the hormone levels of all individuals are updated until the distribution and to remove them from the cluster analysis. Parameters were as follows: \(\alpha_s = 0.4, \gamma = 0.2, \beta_s = 0.001, \alpha_h = 100.0, \beta_h = 0.3, N = 100, q = 4.0, \lambda_i = 3.0,\) and \(\lambda_s = 0.1\).

Step 1. To perform the cluster analysis, the distribution of data should be either random or clumped. Thus, before performing cluster analysis, we calculated \(I_s\)-index (Morisita 1971) to identify the data sets showing uniform distribution and to remove them from the cluster analysis. This is defined as follows:

$$I_s = \frac{p \sum_{i=1}^{N} x_i (x_i - 1)}{\sum_{i=1}^{N} x_i (\sum_{i=1}^{N} x_i - 1)},$$

(5)

where \(p\) determines how many the range of data is divided into and \(x_i\) is the number of individuals in unit \(i\). When \(I_s < 1\), distribution is uniform, whereas when \(I_s > 1\), distribution is clumped (note that when the distribution follows a Poisson distribution, \(I_s = 1\) holds). If the distribution is uniform (\(I_s < 1\)), all individuals are grouped into a single cluster. In such case, the number of clusters was regarded as unity. If \(I_s > 1\), we adopted the following analysis to determine the number of clusters in the population. Note that \(p\) is an arbitrary positive integer, and we set \(p = 7\). We performed the analysis using various values of \(p\) and confirmed that the results were not altered substantively.

Step 2. We classified the distribution of the hormone level in the population by using the gap statistics in the R package cluster (Tibshirani et al. 2001). This package calculates the optimal number of clusters for a given observation on the basis of gap statistics. We adopted the \(k\)-means clustering algorithm to determine the optimal clustering
for a given number of clusters $k$, where $k$ is an integer from 1 to 10. Then the gap statistic was calculated for each $k$, and we identified the optimal number of clusters as the value of $k$ that achieved the maximum gap statistics.

**Results**

*Formation of Multiple Clusters in the Hormone Level Distribution*

Figure 2 illustrates an example of the simulation. Video 1, available online, shows the dynamics of this example. Initially, the hormone level and size of individuals in a population were distributed following a bivariate normal distribution. Once the simulation began, the hormone level increased rapidly for some individuals, whereas for others the hormone level remained low. Individuals became separated into two distinct clusters differing in hormone level. In figure 3a, these are shown by filled and open circles. Body size distribution remained unimodal (fig. 3b). This result was quite similar to the pattern of alternative life-history tactics observed in salmonid (Morita and Nagasawa 2010). Hormonal distribution consisted of some individuals with

![Figure 3](image-url)

*Figure 3:* Distributions of hormone levels and body sizes at the end of the simulation. a. Filled and open circles represent individuals with high and low hormone levels, respectively. Note that circles are separated with regard to hormone levels, but body sizes of the two groups overlapped. b. Number of individuals with different body sizes. Black and white plot bars show individuals with high and low hormone levels, respectively. Individuals with high hormone levels tend to be larger in body size than those with low hormone levels, although their distributions are overlapped. c. Number of individuals with different hormone levels. Two peaks can be observed, representing higher and lower hormone levels, with the latter being widely distributed. The two clusters are separated at about 130. d-f, Results from combining 10 replicates of runs. d. The numbers within each circle distinguish different runs. Filled and open circles represent individuals with high and low hormone levels, respectively. e. Box-whisker plot of body size. Error bars show the range, and bars in the boxes show median value. Body size distribution in which the results of 10 runs were pooled showed a single peak. f. Box-whisker plot of hormone level distribution in which the results of 10 runs were pooled. Distribution of hormone level was bimodal. Parameters were as follows: $\alpha = 0.3$, $\gamma = 0.2$, $\beta = 0.001$, $\alpha_s = 100.0$, $\beta_s = 0.3$, $N = 100$, $q = 4.0$, $\lambda_s = 3.0$, and $\lambda_c = 0.1$. 
markedly high hormone levels and others with low levels (fig. 3c). We expected that the former individuals would achieve earlier sexual maturation. Figure 3d–3f illustrates the results in which 10 runs were pooled, which reveal that the patterns did not substantially change among runs.

Figure 4a shows a heat map of the number of clusters averaged over 10 replicates for each pair of parameters. Vertical and horizontal axes indicate the importance of hormone (\(\lambda_h\)) and body size (\(\lambda_s\)), respectively, to the probability of winning. When both \(\lambda_h\) and \(\lambda_s\) were small, as indicated by “I” in figure 4a, no correlation existed between size and hormone level (fig. 4b). Specifically, the difference in hormone level among individuals was small. When \(\lambda_h\) was larger, the size-hormone distribution showed multiple clusters (fig. 4c). In this case, winners synthesize more hormone than losers, rendering the winner more likely to win the next competition. The positive feedback between behavior and hormone eventually split the population into two or more distinct types of individuals.

As \(\lambda_h\) increased further, the probability of winning strongly depended on the hormone level. This meant that a small difference in hormone level could determine the outcome of the competition; hence, a clear dominance hierarchy was formed depending on the initial hormone level. This resulted in a regular, rather than clumped, distribution of hormone levels, as shown in figure 4d.

The correlation between body size and hormone level increased with an increase in \(\lambda_h\) (fig. 4e). However, a small difference in body size determined the outcome of the competition, resulting in higher rates of both hormone production and size growth. Under this distribution, clustering did not occur because the number of optimal clusters was one. Discrete clusters, as expected for alternative tactics, appeared most clearly when the \(\lambda_s\) was large but not too large, as illustrated in figure 4c. In contrast, only a single cluster was identified when \(\lambda_s\) was small, as illustrated in figure 4b, and also when \(\lambda_s\) was very large, as shown in figure 4d and 4e.

**Figure 4:** Parameter dependence of the dynamics. a. Heat map of the mean cluster number, where darker area shows a larger mean cluster number of hormonal distribution. Roman numbers I–IV correspond to the situation shown in b–e. b–e. Distributions of hormonal levels and body sizes in a population. b. When both \(\lambda_h\) and \(\lambda_s\) are small, the hormonal distribution has a single peak with small variance. Parameters were \(\lambda_h = 0.5\) and \(\lambda_s = 0.0\). c. When \(\lambda_h\) is large, the hormonal distribution exhibits two peaks with multiple clusters. Parameters were \(\lambda_h = 2.5\) and \(\lambda_s = 0.0\). d. When \(\lambda_h\) was too large, the hormone level distribution shows a large variance but has a single peak (cluster number is one). The distribution of body sizes also shows a single peak. Parameters were \(\lambda_h = 15.0\) and \(\lambda_s = 0.0\). e. When \(\lambda_s\) is large, the variance of hormone level becomes larger but the cluster number was one. The hormonal levels and body sizes of individuals become strongly correlated. Parameters were \(\lambda_h = 2.5\) and \(\lambda_s = 15.0\). Other parameters were as follows: \(\alpha_s = 100.0\), \(\beta_s = 0.3\), \(N = 100\), and \(q = 4.0\).
The parameters mediating hormonal dynamics also affect the adoption of alternative tactics in the population. If individuals belonging to the cluster with the highest hormone level will mature and become residents, the fraction of residents in the population will decrease with an increase in the contribution of hormone level to the probability of winning \( \lambda_h \), as illustrated in figure 5. Here \( \lambda_h \) is fixed at 0.5 (see fig. 4a). As \( \lambda_h \) increased, the number of clusters increased, and the number of individuals belonging to the top cluster decreased (figs. 4a, 5). The further increase in \( \lambda_h \) made the cluster disappear, and the number of clusters decreased (fig. 4a).

**Accuracy of Decision-Making**

To examine the stability of the dominance hierarchy and the predictability of life-history choice, we defined the accuracy of decision-making as the probability for an individual to be classified to the cluster predicted from the initial order of hormone level. In figure 6a, as the reaction rate \( q \) increased, the hormone level at the end of simulation more strongly reflected the initial state. The hormone level fluctuated less as the coefficient of reaction rate \( q \) increased (fig. 6b). Because \( q \) mediates the number of encounters with opponents per unit time, the increase in the number of competitions provides more accurate information regarding an individual’s status in the population.

**Discussion**

Numerous classical models of alternative life history assume the existence of threshold values of continuous traits, such as body size, and that distinct patterns of life history are adopted depending on whether the trait is above or below the threshold (Gross 1996; Roff 1996; Tachiki and Koizumi 2016; Horita et al. 2018). Underlying these assumptions are physiological processes realizing life-history choices. From initially similar states, two distinct internal physiological states are eventually formed. In behavioral endocrinology, the positive feedback between hormone level and behavior (e.g., fighting, aggression) has been considered responsible for the process of forming distinct types (Wingfield and Wada 1989; Nelson and Kriegsfeld 2016). In this study, we provided a simple mathematical model as a candidate representation of this process. We assumed that the hormone level constitutes a key factor in decision-making and described the competitive interaction between juveniles and the hormone synthesis of each individual. Notably, the distribution of hormone levels could exhibit multiple discrete clusters, whereas the body size distribution could remain unimodal (i.e., no distinct clusters). This indicates the possibility of discrete clusters of traits (i.e., alternative tactics) arising from a continuous distribution without a threshold rule, as observed in salmonids (Morita and Nagasawa 2010) and also in other organisms (Emlen 1997; Tomkins 1999).

![Figure 5](image_url)  
**Figure 5**: Fraction of residents among juveniles. The results of 10 replicates are shown for each parameter value. Parameters were as follows: \( \alpha_s = 0.3 \), \( \gamma = 0.2 \), \( \beta_s = 0.001 \), \( \alpha_r = 100.0 \), \( \beta_r = 0.3 \), \( N = 100 \), \( q = 4.0 \), \( \lambda_h = 3.0 \), and \( \lambda_s = 0.1 \).

![Figure 6](image_url)  
**Figure 6**: Tendency of changing rank of individuals over time. *a*, Accuracy of decision-making. The results of 10 replicates are shown. *b*, Coefficient of variation (CV) of hormone level CV. The CV decreased with increasing \( q \). Parameters were as follows: \( \alpha_s = 0.3 \), \( \gamma = 0.2 \), \( \beta_s = 0.001 \), \( \alpha_r = 100.0 \), \( \beta_r = 0.3 \), \( N = 100 \), \( q = 4.0 \), \( \lambda_h = 3.0 \), and \( \lambda_s = 0.1 \).
Forming Multiple Clusters within the Distribution of Hormone Levels

The distribution of hormone levels exhibited multiple clusters when the probability of winning was sensitive to the between-individual difference of hormone levels (i.e., \( \lambda_i \) was large but not too large) and when hormonal dynamics processed much more rapidly than the size growth (i.e., \( \alpha_i \) was much larger than \( \alpha(1 + \gamma) \); fig. 4c). After a competitive interaction, the winner synthesizes more androgen and becomes more likely to win in the subsequent fighting. This positive feedback causes the distribution to exhibit multiple peaks. As \( \lambda_i \) is larger, the contribution of hormone level to the probability of winning is stronger and the difference in the probability of winning becomes more pronounced than is the case with small \( \lambda_i \). A strong positive feedback between victory in fighting and enhanced hormone synthesis expands the difference between individuals with initial small differences. Hence, the likelihood of forming multiple clusters within the distribution of hormone levels increases.

In equations (3) and (4), the dynamics of hormone level and body size are qualitatively similar, with both exhibiting a positive feedback loop with the behavioral dynamics (i.e., probability of winning in fighting). Although alternative tactics are characterized by bimodal or multimodal trait distribution of behavior and physiology (Taborsky et al. 2008), we only observed a bimodal distribution with regard to hormone level (fig. 4c). This might be explained in terms of the difference in parameter values that mediate the speed of hormone processing dynamics. It is plausible that hormone levels change more quickly than morphology, such as increase in body size (Lindstedt and Calder 1981). If we assumed that the size growth was much faster than the speed of hormonal processing dynamics (however unrealistic), then the body size distribution became bimodal and the hormonal distribution became unimodal when the probability of winning was controlled by the body size more strongly than by hormone level (i.e., \( \lambda_i < \lambda_b \); fig. S1; figs. S1–S3 are available online). Hence, the multimodal distribution of hormone levels and unimodal distribution of body sizes observed in the wild (Morita and Nagasama 2010) may be the result of differences in parameter values.

A larger weighting factor for the process that responds slower (\( \lambda_i \) in the case of fig. 4e) did not contribute to the formation of multiple clusters. Rather, multiple cluster formation was suppressed with larger weighting factor (see fig. 4e). When the contribution of body size to the probability of winning, \( \lambda_b \), is large, large individuals become likely to win in the competition, and the importance of hormone level toward probability of winning decreases. Hence, an increase in \( \lambda_b \) weakens the feedback between the probability of winning and hormone synthesis, leading to the disappearance of hormone level dimorphism.

Multiple Clusters in the Evolutionary End Point

In the present study, we evaluated a simple mechanistic model for the formation of multiple clusters of a competitive trait (e.g., hormone level). In some publications, the coexistence of multiple types along the spectrum of competitive ability has been discussed as a result of adaptive evolution. When many types continuously compete among one another, the outcome is typically an evolutionarily stable community consisting of discrete and often finite numbers of types. Sasaki and Ellner (1995) derived this result mathematically in the case where the competition kernel between genotypes constituted a Gaussian function of between-genotypes difference in the trait. An elegant result is their mathematical proof of discreteness (in the sense of exact mathematics) when the competition kernel constitutes an analytic function and the resource distribution is not analytic (such as establishing truncation in the high and low ends of resource distributions). In the context of community ecology, a similar pattern was found by Pacala and Tilman (1994), who discussed the limiting similarity of coexisting species. Following these seminal articles, diverse examples of coexisting multiple types have been discussed, including discrete multiple types of phonology of trees (Kubo and Iwasa 1996), mutation rate (Haraguchi and Sasaki 2000), and prey-predator coevolution. In the context of honest signaling of male quality, Johnstone and Grafen (1994) discussed the coexistence of discrete clusters of phenotypes indicating male quality, which answered the puzzle of typical intensity of animal signals in the science of animal behavior. The appearance of multiple clusters of hormonal levels in the present study might be regarded an example of this same general principle.

We note that the results of our study show that multiple clusters of hormone levels might automatically emerge as a result of plausible competitive interaction between individuals in whom no evolutionary adaptation was assumed. This sheds light on an aspect different from that of the numerous theoretical works focusing on adaptive significance. To promote our understanding of the ecological process of alternative tactics, we need to incorporate the studies of molecular mechanisms such as epigenetic control (Champagne 2012) and gene expression (Martin et al. 2010; Johansson et al. 2016) and their association with social interactions and endocrine systems.

Variability of Hormone Levels

The coefficient of variation of the hormone level along the time series decreased with the increase in the frequency of
encounter $q$. When $q$ was smaller, updating of individual status occurred less often and the hormone level fluctuated more strongly. When $q$ was larger, hormone values fluctuated less strongly (fig. 6b) because individuals could estimate their social rank more accurately (see Tachiki and Koizumi 2016). We note that, if the growth rate is small, bimodal size distribution may not be observed before the appearance of matured individuals, and the observed size distribution may have a single peak (Morita and Nagasawa 2010).

Implications for Future Studies

We incorporated hormone level in our model, as this can be experimentally measured to predict future behavior. Hormone levels have been evaluated in previous studies (Devlin and Nagahama 2002; Taves et al. 2009; Munakata 2012). Nevertheless, it would be very useful if we could estimate how androgen contributes to the aggressiveness of individuals and correlates with the probability of winning.

It would also be very informative to understand how juveniles make contact with each other, because considerable behavioral diversity exists among individuals in the same population. In natural situations, individuals may adjust their endocrine systems through contacts that may not be clearly observable. It is therefore necessary to record the behavior of individuals and to quantify parameters such as $q$ and $\lambda$. For example, Butail et al. (2012) reconstructed the trajectory of flying mosquitoes from video data. The estimation of these parameters in fish may thus be possible through the development of specialized measuring devices.

In this study, we demonstrated that dimorphism emerges from the interaction between hormone level and social interaction. Many organisms estimate their own social rank in the population and behave appropriately, considering their status (Taves et al. 2009). Both the nervous and endocrine systems process social information. For example, androgen enhances the aggressiveness of behavior, whereas stress hormones (e.g., cortisol) inhibit behavior. Animals are able to estimate previous experiences and predict future behavior just by measuring their hormone levels. This is likely useful for energetically efficient decision-making, considering the cost of maintaining neural and endocrine systems (Goymann and Hofer 2010). These systems should contribute to understanding biological phenomena that have discreteness. For instance, some birds have partial migration (Wingfield 2005). In male elk, variation in ornaments signals male status and is related to androgen level (Bartos and Bubenik 2011; Bartos et al. 2012). In termites, caste specialization is induced by interaction with other individuals via modification of juvenile hormone titer, and this contributes to the maintenance of the colony (Watanabe et al. 2014). In mandrills, there is a clear hierarchy formed by behavioral interactions and endocrine systems (Setchell 2010).

Nevertheless, in natural conditions, the behavior of animals is likely to be more complex than that assumed herein. For example, hormone level may modify the frequency of encounters among individuals; in turn, this effect may induce polymorphism, which should be considered in future theoretical studies.

We furthermore showed that the ratio of strategies was not substantively affected by the initial condition and environmental fluctuation (figs. S2, S3). This robustness is caused by the feedback between social interactions and hormone synthesis. Decision-making on the basis of social interaction contributes to the stability of a population (Tachiki and Koizumi 2016). Thus, clarifying the relationship between intrinsic states and social interactions along with its ecological consequence is very important to understanding the system.

Conclusion

Behavior and hormone synthesis affect each other; thus, clarifying the relationship between hormonal level and behavior is very important. The data of endocrine status and behavior of the same individual sampled over time are useful to understand the mechanism of decision-making. Ecological sciences would therefore markedly benefit by incorporating endocrinological mechanisms when considering the factors that influence decision-making in animal behavior.

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Statement of Authorship

All authors conceived the study and acquired funding, J.H. provided model analysis and coding simulation, Y.T. and Y.I. provided supervision, J.H. drafted the manuscript, and all authors wrote, reviewed, and edited the manuscript.
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