An Age-Structured Approach to Modelling Behavioural Variation Maintained by Life-History Trade-Offs

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Abstract

There have been numerous empirical studies on the fitness consequences of behavioural syndromes in various animal taxa; however, the ecological and evolutionary implications on a population level are still poorly understood. To better understand these implications, we develop a non-linear age-structured mathematical model to qualitatively examine the evolutionary consequences of a heritable boldness personality trait within an animal population. We assume that this heritable boldness trait is positively correlated with boldness towards predators and intraspecific aggressiveness. This assumption leads to a growth/reproductive success versus mortality trade-off, which is thoroughly investigated and documented in the literature. Another life-history trade-off we include in the model is future versus current reproduction, which was shown by Wolf et al. [1] to be a possible mechanism for the evolution of behavioural syndromes within an animal population. The stability of the system is analysed, whereby the characteristic equation is in the form of a homogeneous Fredholm equation of the second kind which depends on both the perturbation and equilibrium solution. The system is found to be stable due to the competition between individuals of similar boldness acting as a negative feedback mechanism. Using numerical simulations we examine the qualitative features of the solution to the system. In particular, we investigate the interplay between the mutation and competition strength between two individuals with different boldness, whereby we find that an increasing competition range acts to push individuals to both extremes of the shy-bold axis, while an increasing mutation range counteracts this effect. This qualitative trait of aggregation of individuals around the shy and bold extremes is also found when examining different birth, mortality and competition functions.

Introduction

Recent studies suggest that species across a wide range of taxa exhibit behavioural syndromes (also known as animal personality), that is, correlated suites of behaviours across different situations which are also stable across time. This is despite the fact that a high degree of behavioural plasticity would theoretically allow for an individual to maximize their fitness in different situations and environments. Many studies give evidence that behavioural types within a behavioural syndrome are moderately heritable and stable over the entire life of the individual, thereby being a target of natural selection due to their influence on life history strategy (for a review on heritability, see Oers et al. [2]) [3]. For example, Dingemanse et al. [4] found that exploratory behaviour for wild Great Tits (*Parus Major*) was both repeatable and heritable, and unrelated to age, body condition or sex. This was found to influence important life-history traits such as offspring production, recruitment rates and survival, which implies that personality in Great Tits is selected upon, leading to evolutionary change. In addition to heritability, there is strong support that phenotypic correlations between components of personality often originate from strong underlying genetic correlations. A well documented example is the strong correlation between boldness towards predators, high activity level and intraspecific aggressiveness observed in various animal taxa [5–8].

A fundamental behavioural type is the shy-bold continuum, where boldness is defined to be the propensity for an individual to take risks [9–12]. This behavioural type has been documented in over 60 species across multiple taxa, suggesting its importance as a component of animal personality, particularly due to empirical studies often finding that boldness is consistent across multiple contexts (but see Sinn & Moltchaniwskyj [13]). Studies give evidence that an individual’s position on the shy-bold axis often correlates with crucial life-history traits such as reproduction and survival, due to its correlation with related traits such as antipredator behaviour, mate choice, intraspecific aggression, growth, body mass, foraging behaviour, exploration/dispersal behaviour, recruitment and social behaviour [14,15].

Moreover, crucial behavioural types such as shy-boldness influence and reflect important life-history trade-offs, such as growth versus mortality, mortality versus reproductive success and current reproduction versus future reproduction. For example, in stickleback fish populations, individuals that are more aggressive towards conspecifics are also bolder towards predators. While a high level of intraspecific aggressiveness is instrumental in gaining resources (mates, food etc.), the correlated antipredator boldness may incur an increased mortality risk [6,16].

Although there have been a large number of empirical studies which have investigated shy-boldness across multiple contexts and the fitness consequences in various animal taxa, there have been
very few studies which examine, particularly from a mathematically qualitative perspective, the evolutionary and ecological implications that shy-bold personality variation has on a population. Examples include life history and demography, dispersal and invasion speeds, speciation and disease spread (see Wolf & Weissing [17] for a detailed review on such implications). However, to understand the implications there must first be a framework on the more fundamental question of how shy-bold variation is maintained within a population and how it evolves over time. There are a few hypotheses in the literature which attempt to answer this; for example, a density- and frequency-dependent selection model or a similar model which includes phenotypic plasticity (Wilson et al. [10]) or a life-history trade-off model (Wolf et al. [1], Reale et al. [19]). In this study, we focus on the latter, in particular a trade-off between current and future reproductive success as proposed by Wolf et al. [1]. This postulates that an asset protection principle drives the evolution of personality variation; individuals with high future reproductive expectations are more risk-averse than individuals who have low future reproductive expectations. Using an agent-based model, Wolf et al. [1] showed that a dimorphism in an inheritable exploration trait, whereby individuals who explore the environment thoroughly invest in future reproduction/fitness and individuals who explore the environment superficially invest in current reproduction/fitness, results in a polymorphism in traits, such as antipredator boldness and intraspecific aggressiveness.

We formulate a continuous age- and boldness-structured model based on two life-history trade-offs: current versus future reproduction as proposed by Wolf et al. [1], and also mortality versus growth/reproductive success, which is due to the positive effects of intraspecific aggressiveness and the negative effects of antipredator boldness. Instead of assuming a heritable exploration trait as in the study by Wolf et al. [1], we assume that shy-boldness is heritable and is directly correlated with exploratory behaviour, in line with the commonly identified exploratory-boldness behavioural syndrome in empirical studies [9,20]. Thus, shy individuals are thorough explorers who invest in future reproduction and suffer low risk of mortality, while bold individuals are superficial explorers who invest in current reproduction, but incur a greater mortality risk due to predation associated with inappropriate boldness.

Methods

Model Formulation

The boldness of an individual is given by $x \in [0,1]$, whereby $x = 0$ and $x = 1$ correspond to the extremes of shy and bold behaviour, respectively. We denote $u(a,x,t)$ to be the frequency of individuals of age $a$ with boldness $x$ at time $t$ and use the McKendrick-von Foerster equation to model the age structure, given by

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a,x)u(a,x,t),$$

with boundary condition

$$u(0,x,t)=\frac{1}{\Phi(x,t)}\int_0^{\infty} b(a,\tilde{x})N(x,\tilde{x},\sigma_1)u(a,\tilde{x},t)d\tilde{x}$$

and initial condition

$$u(a,x,0)=f(a,x),$$

where $b(a,x)$ is the birth function, $N(x,\tilde{x},\sigma_1)$ is the mutation function, $\Phi(x,t)$ is a function governing competition between individuals, $\mu(a,x)$ is the mortality function and $2\Lambda_0$ is the total fertile period of an individual. We give a specific form for each of these functions below, but also consider alternative forms for these functions in the subsequent sections to show how they can affect solutions.

We define the birth function $b(a,x)$ to be

$$b(a,x)=(2+x)\left(\frac{(1-x)+xe^{-(a-\alpha_0)}}{1+e^{-(a-\alpha_0)}}\right).$$

The factor $\left(\frac{(1-x)+xe^{-(a-\alpha_0)}}{1+e^{-(a-\alpha_0)}}\right)$ is defined such that shy individuals reproduce towards the end of their fertile periods, while bold individuals reproduce at the start of their fertile periods. The $(2+x)$ factor represents the increase in reproduction gained from a given boldness value due to aggressive behaviour when competing against conspecifics for resources (food, mates). Specifically, it increases with respect to boldness and represents

Figure 1. Birth and mortality functions. Panel A and B show $b(a,x)$ and $\mu(a,x)$ respectively. These two functions are defined such that they reflect the future versus current reproduction and growth/reproduction success versus mortality life-history trade-offs.
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the maximum number of offspring which an individual can have for a given boldness \( x \). In particular, an individual with boldness \( x = 0 \) will have 2 offspring, whereas an individual with boldness \( x = 1 \) will have 3 offspring. See Figure 1 for a plot of \( b(a, x) \).

The factor \( N(x, x, \sigma_1) \) dictates mutation of the offspring, resulting in different boldness values than their parents, where \( N(x, y, \sigma) \) is a normal distribution with mean \( y \) and standard deviation \( \sigma \), that is,

\[
N(x, \mu, \sigma) = \frac{1}{\sqrt{2\pi}\sigma} \exp \left[ -\frac{(x - \mu)^2}{2\sigma^2} \right].
\]  

The competition experienced by an individual with boldness value \( x \) at time \( t \), due to other individuals adopting similar strategies as a consequence of their boldness, is denoted by \( \Phi(x, t) \). It is defined as

\[
\Phi(x, t) = 1 + \int_0^t \int_0^{2a_0} N(x, x, \sigma_2) u(a, x, t) da dx,
\]

where \( \sigma_2 \) represents the strength of competition between two individuals with different boldness levels. The competition factor in the boundary condition Eq. (2) serves to reduce reproduction rates if there are too many individuals adopting similar strategies by having similar boldness values.

Finally, the mortality function \( \mu(a, x) \) is given by

\[
\mu(a, x) = \left( \frac{a}{2a_0} \right)^{9-x} + \left( \frac{x}{4} \right) \left( 1 - \frac{a}{2a_0} \right).
\]  

The mortality function \( \mu(a, x) \) is defined such that shy individuals suffer the least mortality due to their risk-averse behaviour towards predators, in contrast to bold individuals who suffer the greatest mortality due to risk-prone behaviour towards predators. The left term accounts for an intrinsic mortality that is higher for bolder individuals and increases with respect to age due to senescence. The right term represents the penalty for a given level of boldness, where mortality is higher for bolder individuals and decreases with respect to age. This is illustrated in Figure 1. Note that \( \mu(a, x) \) represents a mortality rate and not a probability of mortality; as such \( a = 2a_0 \) is the maximum fertile age, not the maximum life span. Thus, Eq. (7) implies that the average remaining life span after an individual’s fertility period is 1 day.

Throughout this study we set \( a_0 = 5 \), \( \sigma_1 = 0.02 \), \( \sigma_2 = 0.15 \) and initial condition \( f(a, 0.5) = 1 \), for \( a \in [0,1] \), and zero everywhere else. Thus, individuals have a maximum lifespan of 10 years and begin

Figure 2. Evolution of the population over time. The system was numerically simulated using an Upwind scheme and stopped at certain \( t \) values. Panels A, B, C and D correspond to \( t = 10, 30, 60 \) and 120 respectively. Bold individuals appear to experience the fast growth due to the future versus current reproduction trade-off. doi:10.1371/journal.pone.0084774.g002
in cohorts of age 0 to 1 with an intermediate boldness level of \(x = 0.5\).

**Results**

**Stability Analysis**

The solution to Eq. (1) is given by

\[
\begin{align*}
    u(a,x,t) &= \left\{ 
    \begin{array}{ll}
        u(a-t,x,0) \exp\left(-\int_{a-t}^{a} \mu(s,x) \, ds\right) & \text{if } a \geq t \\
        u(0,x,t-a) \exp\left(-\int_{0}^{a} \mu(s,x) \, ds\right) & \text{if } a < t.
    \end{array}
    \right.
\end{align*}
\]  

(8)

We denote the stable age and boldness distribution to be \(\bar{u}(a,x)\), which is given by (via substituting into the McKendrick-von Foerster equation)

\[
\frac{\partial \bar{u}}{\partial a} = -\mu(a,x)\bar{u} = \bar{u}(0,x) \exp\left(-\int_{0}^{a} \mu(s,x) \, ds\right).
\]  

(9)

First we examine the boundary condition without the competition factor, which makes the boundary condition, and consequently the system, linear. We test stability by letting \(u(a,x,t) = \bar{u}(a,x)e^{\lambda t}\). This gives

\[
\bar{u}(a,x) = \bar{u}(0,x) \exp\left(-\lambda a - \int_{0}^{a} \mu(s,x) \, ds\right).
\]  

(10)

and the boundary condition Eq. (2) becomes

\[
\frac{\partial \bar{u}}{\partial a} = -\mu(a,x)\bar{u} = \bar{u}(0,x) \exp\left(-\int_{0}^{a} \mu(s,x) \, ds\right).
\]  

(9)
By biological reasoning, the existence of the competition factor $W(x,t)$ as a negative feedback must be crucial to the stability of the equilibrium $u(a,x)$. Note that the dependence on boldness $x_i$ in particular mutation along the shy-bold axis, means that another approach is needed to analyse the stability than the case of classical linear age-structured models. Mathematically analysing the stability of Eq. (1) with boundary condition Eq. (11) can be achieved by employing classical Fredholm theory [21,22]. Fredholm’s first and second theorem state that Eq. (11) has a non-trivial $u(0,x)$ with eigenvalue $\lambda$ if and only if $\phi = 1$ is a zero of

$$D(\phi) = 1 + \sum_{p=1}^{\infty} \left(\frac{-\phi}{p!}\right) c_p,$$

where

$$c_p = \int_0^a \cdots \int_0^a K\left(\frac{x_1 s_2 \ldots s_p}{x_1 s_2 \ldots s_p}\right) ds_1 ds_2 \ldots ds_p,$$

Figure 4. 2D Comparison of solutions with different $\sigma_1$ and $\sigma_2$. The system was numerically simulated using an Upwind scheme until the solution reached an equilibrium state and then integrated along the age axis for simplification. Hence, frequency here is a measure of the total population of a certain boldness value. See also Figure 3.

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The kernel $K(x, y)$ used in this model is a bounded and integrable function, which was proved to be a sufficient condition for the series in Eq. (12) to converge for all $\lambda$ [21]. Numerically, we find that $D(1)$ is monotonically increasing as $\lambda$ increases due to the $e^{-\lambda s}$ term in the integrand of Eq. (15), that is, $\frac{dD(1)}{d\lambda} > 0$ for $\lambda > 0$, with an asymptote at $D(1) = 1$. Thus, if $D(1) < 0$ for $\lambda = 0$, then there exists some $\lambda > 0$ for which $D(1) = 0$. Numerically computing the first few significant terms of Eq. (12), we can show that $D(1) < 0$ for $\lambda = 0$ and that $\lambda \approx 16.2$ satisfies Eq. (12). This indicates that the system reaches a stable age and shy-boldness distribution which either increases or decreases exponentially (depending on the form of the birth, mortality, competition and mutation functions) when there is an absence of competition, as expected from linear age-structured population modelling theory.

For the full problem, where the competition factor is included, we first observe that the solution cannot be unbounded, regardless of $\phi = 1$ is a zero of multiplicity $m$ of $D(\phi)$, then Eq. (11) possesses at least one, and at most $m$, non-trivial linearly independent solutions.

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of the possibility of local instability, due to the following upper bound:

\[
\pi(0,x) = \frac{1}{\Phi(x,t)} \int_0^t \int_0^\infty b(a,\tilde{x})N(x,\tilde{x},\sigma_1)\pi(0,\tilde{x})\exp\left(-a\tilde{x} - \int_0^{\tilde{x}} \mu(s,x)ds\right) d\tilde{x} dx \\
\leq \max |b(a,x)| \max |N(x,\tilde{x},\sigma_1)| \min |N(x,\tilde{x},\sigma_2)| .
\]

To investigate the local stability, we linearise the boundary condition by letting \(u(a,x,t) = \tilde{u}(a,x) + u(a,x,t)\), where \(u(a,x)\) denotes the equilibrium solution and \(\tilde{u}(a,x)\) denotes a small perturbation. Substituting this into the boundary condition and linearising, we obtain

\[
\tilde{u}(0,x,t) = \frac{\frac{1}{\Phi(x,t)} \int_0^t \int_0^\infty b(a,\tilde{x})N(x,\tilde{x},\sigma_1)\tilde{u}(0,\tilde{x})d\tilde{x} dx}{1 + \frac{1}{\Phi(x,t)} \int_0^t \int_0^\infty N(x,\tilde{x},\sigma_2)\pi(0,\tilde{x})d\tilde{x}}.
\]

Then, we test the growth of the perturbation by setting \(\tilde{u}(a,x,t) = \exp(\lambda t)\), where \(\lambda\) is the eigenvalue of the linear operator \(L(u) = -\mu(a,x)u(a,x,t) - u_0(a,x,t)\) and \(\tilde{u}(a,x)\) is the corresponding eigenfunction. Substituting this into Eq. (1), we find that \(\tilde{u}\) satisfies

\[
\tilde{u}(a,x,t) = \exp(\lambda(t-a) - \int_0^0 \mu(s,x)ds). \]

Using Eq. (3) and Eq. (9), we obtain

\[
\tilde{u}(0,x) = \int_0^t \tilde{u}(0,\tilde{x})G(x,\tilde{x},\lambda)d\tilde{x},
\]

where

\[
G(x,\tilde{x},\lambda) = \frac{\int_0^t \exp(-\lambda t - \int_0^t \mu(s,x)ds) \int_0^\infty b(a,\tilde{x})N(x,\tilde{x},\sigma_1)\pi(0,\tilde{x})d\tilde{x}}{1 + \int_0^t \int_0^\infty N(x,\tilde{x},\sigma_2)\pi(0,\tilde{x})d\tilde{x}}.
\]

Again, the eigenvalue is determined by a homogeneous Fredholm integral equation, with \(G(x,y,\lambda)\) as the kernel. Note that at the trivial equilibrium \(\tilde{u} = 0\), Eq. (20) reduces to the kernel for the linear case without competition Eq. (15), thus \(\tilde{u} = 0\) is locally unstable, as we have determined above. For the non-trivial equilibrium, we can reuse the argument for the case without the competition factor to deduce stability. However, note that explicitly calculating \(\lambda\) in this case is more difficult than the case without the competition factor because of the dependence on the equilibrium solution \(\tilde{u}(0,x)\) in the integral equation, for which we have no closed form. From numerical simulations, such as the one shown in Figure 2, we can see that the system has a stable non-trivial equilibrium. This is reaffirmed by numerically obtaining the long-term steady state \(\tilde{u}(0,x)\) and substituting into Eq. (20) to find that \(D(1) > 0\) for \(\lambda = 0\), which implies that there does not exist a \(\lambda \geq 0\) such that \(D(1) = 0\). Thus the system is locally asymptotically stable.

Simulations and Other Forms of \(b(a,x)\) and \(\mu(a,x)\)

The effect of competition as a negative feedback not only induces stability in the equilibrium solution but also qualitatively affects the form of the solution, as shown in Figure 3 and Figure 4. The table of figures illustrates the relationship between mutation and competition, in particular how varying their values will alter the distribution of the population across the shy-bold continuum. Most notably, an increase of the competition range \(\sigma_2\) has the effect of polarising individuals to either side of the shy-bold continuum, whereas an increase in the mutation range \(\sigma_1\) acts to counter this by spreading the population more evenly across the shy-bold axis.

Depending on the form of the birth \(b(a,x)\) and mortality \(\mu(a,x)\) functions, it is possible for \(\lambda\) in Eq. (20) to have an imaginary part and thus render \(\tilde{u}(a,x)\) to be periodic. However, this is unlikely for smooth forms of \(b(a,x)\) and \(\mu(a,x)\), due to the requirement of Eq. (12); if \(\lambda\) were to have a finite imaginary component, then there is the extra condition of the imaginary component of the series to converge to zero. In general, we have found that only non-smooth \(b(a,x)\) of a form similar to

\[
b(a,x) = \delta(a-a_0).
\]

allows for a periodic solution, as shown in Figure 5.

We simulate the two cases where there is only future versus current reproduction trade-off and only growth/reproductive success versus mortality trade-off. These are shown in panel A of Figure 6 and panel B of Figure 6 respectively. The simulations indicate that either case reaches a stable equilibrium. Notably, both cases share the same qualitative feature of having isolated peaks at both shy and bold extremes.

For only future versus current reproduction, we change the birth and mortality functions to

\[
b(a,x) = z\left(\frac{1-x}{1+x}\right),
\]

\[
\mu(a,x) = \exp\left[\frac{5}{1 + e^{-\left(a-a_0\right)}}\right].
\]

For only growth/reproductive success, we change only the birth function to

\[
b(a,x) = z\left(\frac{2+x}{2}\right).
\]
Studies on animal personality, in particular the shy-boldness behavioural type in animals, have observed that there are life-strategy trade-offs due to repeatability of behaviour and limited behavioural plasticity across contexts, despite the advantages of a flexible behavioural response. Many studies in the literature recognise that these trade-offs may have important ecological and evolutionary implications for an animal population, yet there have been very few mathematical studies to qualitatively examine this [23]. Using an agent-based model, where individuals participate in several games in each time step, Wolf et al. [1] demonstrated that a population dimorphism for an exploration trait (either a very thorough or superficial explorer), driven by a life-history trade-off, corresponded to a behavioural syndrome within the population, specifically, a correlation between exploration, boldness and aggressiveness. Furthermore, using a discrete mathematical model, they showed that this dimorphic population is stable over time, that is, it is protected from invasions by mutant individuals. In this study, we have presented a continuous age- and boldness-structured model with the aim of giving a qualitative insight into the evolutionary implications of a shy-boldness behavioural type maintained via a similar life-history trade-off within a population.

The functions used in this model were designed to be mathematically elegant yet roughly conforming to reality. Different forms of these functions, particularly the normal distributions used in the competition and mutation factors, could change the qualitative features of the solution dramatically. The normal distribution is perhaps a suitable representation for mutation rates in reality, and promisingly, there have been efforts to quantify the heritability of behavioural types (see Dingemanse & Reale [23] and references therein). However, competition between shy-bold individuals, assuming a boldness-aggressiveness behavioural syndrome, is not likely to be dictated by a normal distribution. Instead, it is likely to be represented by a distribution that is skewed towards bold individuals, as shy individuals, by our definition, are not as aggressive as bold individuals are. Moreover, an individual is more likely to be successful when competing against other individuals with lower boldness. Thus, a more
realistic form is the skew normal distribution (shown in Figure 7), given by

\[
\mathcal{N}(x; \mu, \sigma, \alpha) = \frac{1}{\sqrt{2\pi \sigma}} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) \text{erfc}\left[\frac{x-\mu}{\sqrt{2\sigma}}\right].
\] (24)

As shown in Figure 8, this gives rise to qualitatively different solutions to those generated by the competition function using a normal distribution, since there is more incentive for individuals to be bold.

On the other hand, further assume that shy individuals are less competitive than bold individuals. This can be modelled by simply multiplying Eq. (24) by a factor of \((a+x)\), where \(a > 0\) controls the difference in competition strength of shy and bold individuals. We set \(a = 0.5\), which gives a competition function of the form

\[
\Phi(x) = 1 + \frac{1}{2} (1 + 2x) \int_{0}^{\frac{x}{2}} \mathcal{N}(x; \mu, \sigma, \alpha) \mathrm{d}x \mathrm{d}\alpha.
\] (25)

This generates solutions where the qualitative feature of two peaks at both shy and bold extremes is more evident, as shown in Figure 9. In a similar vein, different forms of the distribution for peaks at both shy and bold extremes is more evident, as shown in Figure 8. In a similar vein, different forms of the distribution for peaks at both shy and bold extremes is more evident, as shown in Figure 8.

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