Theoretical study for evolution of signal, sensor, and decision making

里居, 伸祐

https://hdl.handle.net/2324/2236050

出版情報：Kyushu University, 2018, 博士（理学）, 課程博士
バージョン：
権利関係：

Theoretical study for evolution of signal, sensor, and decision making

Shinsuke Satoi

Submitted in partial fulfillment of the requirements
for the degree of
Doctor of Science
In Graduate School of System Life Sciences,
Kyushu University.
January, 2019

Contents

Preface

Animals sense signals from physical and biological environments to make decisions critical for their survival and reproduction. Some animals emit signals for attracting prey and mate or avoiding predators. There are animals that sense and respond these signals to gain the benefit or reduce the fitness loss resulting from the interaction with signal senders. A series of studies about how and when signals organisms emit, which sensors organisms have evolved, and how organisms select their behaviors in response to signals are called "sensory ecology". In recent years, sensory ecology becomes an increasingly popular research area (Stevens 2013).

Interactions between signal senders and signal receivers start when signals are emitted. This step is called "signaling". In the field of behavioral ecology, communication takes place when some signals are emitted by an individual in order to change the behavior of other individual(s) (Wilson 1975). The signals are highly diverse: they can be visual (i.e. coloration, shape), chemical (i.e. smell, pheromone), or auditory (i.e. voice, buzzing) (Endler 1992; Chivers and Smith, 1998; Partan and Marler, 2005; Goepfert and Henning 2016). Signals would be optimized to increase fitness of the signal sender during evolution. The evolution of signals is well studied in mimicking organisms. Some organisms mimic the signal emitted by others to cheat other individuals to increase survival and reproductive success (Ruxton et al. 2004). Many species of *Eristalis* mimic color patterns of distasteful bees for avoiding predation by birds (Rettenmeyer 1970), and parasitic ants steal food items from other colonies by mimicking smells of other colonies (Dettner & Liepert, 1994). In contrast, emitting signals may be sometime costly as it would increase predation risks. Haff and Magrath (2011) reported that the begging calls of birds attract predators, increasing the predation risk . Understanding the trade-off between benefit and cost of signal emission is the critical issue in sensory ecology.

After signals are emitted, the signals need to be received by other individual(s) who may or may not be conspecifics of the signal sender. This step is called "sensing". Sensors are highly diversified because of the demand to receive a variety of signals. To receive light signals effectively, the animal needs to have light sensors (eyes). To discriminate colors, an animal must have a sensor which reacts the specific wavelength (color vision). To detect shapes, an animal must have light sensors with sufficiently high resolution. In the process of sensing, organisms pick out a part of environmental information even if they receive an overwhelming amount of stimuli from environment (Stevens 2013). Communication and subsequent behaviors do not occur if sensors do not match signals. The characters of each sensor such as a detectable wavelength have been studied for a long time. The reason why animals have evolved each specific sensor is being studied in sensory ecology in recent years. Evolutionary histories of sensors are well discussed in a simple system such as the relationship between the chemical sensors of pollinator and chemical signals from flowers (Bromenshenk et al 2015). Which sensors organisms have and the reason why the sensors have evolved are another important question in sensory ecology.

After organisms receive signals, they select appropriate behaviors. This step is called "decision making". Decision making has been studied not only in ecology and animal behavior but also in psychology and economics. An example of decision making can be found even in a simple organism. Bacteria change their orientation when they receive some chemical signals (Adler 1975). Higher organisms process the signals and information in nerve systems and make appropriate decisions based on their experiences and situations. When animals select foraging patches, they decide whether to move away from the patch or stay by predicting their future benefit and cost based on their experiences (Pyke et al., 1977). However, how animals make decisions under more complicated biological interactions remain unresolved. Understanding the mechanism of decision making under complex situations is the final goal in sensory ecology.

The types of signals, characters of sensors, and styles of decision-making may differ depending on species, habitats and individuals. Many experiments have been conducted for different species, and the knowledge about the characteristics of signals, sensors, and decision making of organisms have been accumulated rapidly.
Theoretical studies for decision making have been performed for a long time (e.g. Staddon and Gendron 1983; Jones 1978). However, only a small number of theoretical studies about sensors and signals have been performed, which is in sharp contrast with a wealth of experimental studies accumulated in sensory ecology. General and commonly used ways to study sensor and signals with mathematical models do not exist, though there are many frameworks for considering the problem of decision making. It is clear that theoretical studies are necessary for understanding the evolution and adaptation of sensors and signals. Theoretical frameworks that integrate three important processes, signaling, sensing, and decision making, are increasingly demanded.

In this thesis, I report my theoretical studies on each important question in sensory ecology: signaling, sensing, and decision making. In chapter 1 and 2, I constructed mathematical models for the evolution of singles and sensors based on interactions via chemical and visual signals. In chapter 3, I constructed a mathematical model that integrates evolution and learning in decision making. These studies will open a new window to study animal behaviors from the view point of sensory ecology. In the following, I summarize the contents of each chapter:

Chapter 1: Chemical mimicry or crypsis–the evolutionary game played by parasitic ants invading other colonies

Some ant species are specialized parasites that invade the nests of other ants and steal their food, larvae, and eggs. To be successful, they must evade detection by patrolling hosts who attack invaders. Ants distinguish invaders from individuals of their own nest through the cuticular hydrocarbon profile, as their nestmates have a similar mixture of coating chemicals. To circumvent this, some parasites adopt mimicry, using a mixture of chemicals that has a similar composition to that of their hosts, while others adopt crypsis, with a reduced amount of chemicals. Here we develop a mathematical model to describe the conditions under which each of these strategies evolves, assuming that the parasites and hosts are ants with their own colonies. Host ants distinguish their nestmates from parasites through differences in their chemical traits, which are represented in multi-dimensional space. Parasitic ants engage in competition with other conspecific colonies, which is more intense between colonies with similar chemical traits, jeopardising the advantage of cryptic parasites. We then define parasites' fitness with respect to chemical profiles and discuss the evolution of their chemical strategies. Cryptic parasites evolve when competition among colonies is weak, when many types of host colonies exist, and when host recognition accuracy is high. Mimetic parasites evolve under the opposite conditions.

Chapter 2: When Faster Moving Animals should Have Better Visual Ability?-- Computational Study of Leuckart's Law.

Leuckart's Law states that among vertebrates, swifter animals should have larger eyes. A positive correlation between movement speed and eye size is a plausible hypothesis because faster-moving animals need to have a higher level of visual acuity to recognize food items and obstacles while they are still far away and because the ability of eyes to resolve images is known to increase with their size. A small number of empirical studies suggest that Leuckart's Law is supported for mammals but rejected for birds. We ask, when faster moving animals should have better visual ability? We conducted computer simulation studies of an animal moving on a plane that contains many food items as well as obstacles. The animal moves at a constant speed but changes its directional angle when it recognizes food items or obstacles. We examined the number of food items the animal consumed and the number of obstacles it collided with. Given a small cost of visual acuity, we obtained the optimal visual acuity, which depended on several parameters such as visible distance, visible angle, turning ability, movement speed, and densities of foods and obstacles in the field. Assuming that the animal's visual acuity is close to the optimal value predicted by the model, Leuckart's Law mostly holds when animals are in an environment with similar densities of food items and obstacles. The positive correlation between movement speed and visual distance was stronger with more obstacles and fewer food items. However, Leuckart's Law may not hold if food is abundant, obstacles are rare, and collision damage is small.

Chapter 3: An integrated theoretical framework bridging evolution and learning behaviors in response to uncertain signals

Animals receive many signals from the environment, and use these signals to decide their behavior. Many studies discuss how animals decide their behavior in response to signals, with many theoretical studies focusing on this problem. Many animals decide their actions based on both innate traits and their experience. However, the question on when animals adopt innate decision-making and when animals behave based on their experience remain. It is difficult to resolve this question using existing mathematical models. Here, we constructed a mathematical model that included decision-making using both innate and learning behaviors by extending the Bayesian learning model. In particular, we assumed an initial prior distribution in the learning model as an evolutionary trait. This approach allowed us to construct a simple framework to consider decision-making by both innate and learnt behavior. Furthermore, we applied this model to avoidance behavior, and analyzed when animals avoid signals innately and when animals avoid signals by using their experiences. We showed that innate avoidance evolves when the cost of attacking signals and the frequency of the signal is high. In contrast, animals avoid signals based on experiences under the opposite conditions.

References

Adler, J. (1975). Chemotaxis in bacteria. *Annual review of biochemistry*, *44*(1), 341-356.

Bromenshenk, J., Henderson, C., Seccomb, R., Welch, P., Debnam, S., & Firth, D. (2015). Bees as biosensors: chemosensory ability, honey bee monitoring systems, and emergent sensor technologies derived from the pollinator syndrome. *Biosensors*, *5*(4), 678-711.

Chivers, D. P., & Smith, R. J. F. (1998). Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. *Ecoscience*, *5*(3), 338-352.

Dettner, K., & Liepert, C. (1994). CHEMICAL MIMICRY AND CAMOUFLAGE. *Annual Review of Entomology*, *39*, 129-154.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist*, *139*, S125-S153.

Goepfert, M. C., & Hennig, R. M. (2016). Hearing in insects. *Annual Review of Entomology*, *61*, 257-276.

Haff, T. M., & Magrath, R. D. (2011). Calling at a cost: elevated nestling calling attracts predators to active nests. *Biology Letters*, *7*(4), 493-495.

Jones, P. (1978). On the two armed bandit with one probability known. *Metrika*, *25*(1), 235-239.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619-640.

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist*, *166*(2), 231-245.

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *The quarterly review of biology*, *52*(2), 137-154.

Rettenmeyer, C. W. (1970). Insect mimicry. *Annual Review of Entomology*, *15*(1), 43-74.

Ruxton, G. D., Sherratt, T. N., Speed, M. P., Speed, M. P., & Speed, M. (2004). *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*: Oxford University Press.

Staddon, J., & Gendron, R. P. (1983). Optimal detection of cryptic prey may lead to predator switching. *The American Naturalist*, *122*(6), 843-848.

Stevens, M. (2013). *Sensory ecology, behaviour, and evolution*: Oxford University Press.

Wilson, E.O. (1975). Sociobiology: the new synthesis, Harvard University Press.

Chapter 1

Chemical mimicry or crypsis–the evolutionary game played by parasitic ants invading other colonies

The study of this chapter, done in collaboration with Dr. Yoh Iwas, was accepted in Theoretical Ecology in 2018

Introduction

Under mimicry, an organism (called a mimic) simulates another organism (called a model), and a third organism identifies the mimic as an example of the model (Dettner & Liepert, 1994). Animals adopt mimicry to avoid attack by other animals or to successfully attack their prey. Many observations suggest that it provides the mimetic organism some fitness benefit. For example, ant-mimicking jumping spider of genus *Myrmarachne* reduce the chance of being eaten by larger jumping spiders (Haung et al., 2010). Animals may improve the effectiveness of attacking their own prey through 'aggressive mimicry' (Stevens, 2013). For example, bluestriped fangblennies (*Plagiotremus rhinothynchos*) mimic juvenile cleaner wrass (*Labroides dimidiatus*), which remove ectoparasites from the bodies of other coral reef fishes, allowing them to approach coral reef fishes and obtain their body tissues as food (Cheney, 2012). These mimics have body colourations and behaviours similar to those of the model, making their victims accept them.

Nearly all animals, especially terrestrial arthropods, use chemical cues to communicate with other members of their species and to perceive individuals of other species, such as prey, predators, or competitors. Consequently, many organisms employ 'chemical mimicry' (Pasteur, 1982), whereby they simulate chemical cues to avoid predation or to effectively attack other animals. For example, the blister beetle (*Meloe franciscanus*) parasitises nest of a solitary bee (*Habropoda pallida*) by exploiting its chemical cues (Saul-Gershenz & Millar, 2006). Female *H. pallida* emit sex pheromones that attract male bees searching for mates. Blister beetles attract male *H. pallida* using pheromone-like chemicals that mimic those emitted by female bees to invade the bees' nest by attaching to the attracted males.

Chemical mimicry associated with the recognition of nestmates and parasites by ants is well studied. Ants distinguish their nestmates from non-nestmates through cuticular hydrocarbon profiles on their bodies (Singer, 1998; Akino et al., 2002, 2004; Howard &

Blomquist, 2005; Ozaki & Wada-Katsumata, 2010), which are usually exchanged whenever ants encounter each other in the same colony. Consequently, individuals from different colonies can be distinguished by their chemical profiles, allowing invaders to be detected and removed or immediately killed.

Some ant species are specialised parasites that can invade other colonies by mimicking the odour of the host. Following invasion, these parasitic species exhibit several alternative behaviours, such as [1] coexisting with host ants in the same nest (Ward, 1996; Maschwitz et al., 2000; Sumner et al., 2003), [2] taking over the host colony (Topoff & Zimmerli, 1993; Mori, D'Ettoree, & Le Moli, 1995); [3] laying and rearing their eggs in the host nest (Maschwitz et al., 2004; Witte et al., 2009; Lhomme et al., 2012); and [4] stealing resources from the host nest and transporting them to their own colonies (Perfecto & Van der Meer, 1993; Breed et al., 2012).

Species parasitising ant nests adopt different chemical mimicking strategies, which we classify as 'chemical mimicry' and 'chemical crypsis', following Dettner and Liepert (1994), Lenoir et al., (2001), von Beeren et al., (2011), and Kilner & Langmore (2011). Chemical mimicry implies the chemical resemblance of another species through the biosynthesis of chemical cues or the acquisition of chemicals from host colonies. Host ants accept mimetic parasites because they have similar recognition cues. In contrast, chemical crypsis implies a lack of such cues. Ants have low levels of cuticular hydrocarbons immediately after emergence and gain colony-specific chemical cues during growth (Fielde, 1905; Lenoir et al., 1999; Lenoir et al., 2001). Hence, host ants do not distinguish cryptic parasites from their own young workers. Consequently, host ants readily accept cryptic parasites. Thus, crypsis is considered an effective invasion strategy (Kilner & Langmore, 2011).

Some species are known to adopt both strategies. For example, *Acromyrmex insinuator*, a parasitic ant, is chemically insignificant when they invade host colonies and then gradually acquire host colony-specific chemical profiles (Nehring et al., 2015).

Many theoretical investigations have been done on the role of mimicry in host-parasite systems (e.g. Gavrilets, 1997; Rodriguez-Girones & Lotem, 1999), particularly brood parasites such as cuckoos and parasites of ants. However, to our knowledge, published research does not consider the evolution of traits in parasites employing a cryptic strategy.

In this paper, we construct a mathematical model to investigate the conditions for crypsis and mimicry to evolve in the chemical strategies of parasitic ants. We define the fitness of a parasite according to the chemical profiles, and discuss the evolution of diverse chemical strategies. We show that cryptic parasites evolve when colonies weakly compete, when many types of host colonies exist, and when hosts recognise parasites with high accuracy. Mimetic parasites evolve under the opposite conditions.

Model–the chemical profile game

Figure. 1 illustrates the model. Assumptions are: parasites and hosts are ants with their own colonies; colonies of the same parasitic species exist in the same habitat and easily contact each other; parasitic ants steal resources from the host nests and return them to their own nests; host ants distinguish their nestmates from non-nestmates through their chemical profiles and parasites employ chemical strategies to trick host ants and sneak into their colonies.

We consider two multi-dimensional chemical traits as follows: $\boldsymbol{x}$ represents a vector (x_1, x_2, …, x_n) of the chemical traits of the host colony, and $\boldsymbol{y}$ represents a vector (y_1, y_2, …, y_n) of the chemical traits of the parasite. We define the two parasitic strategies as follows: mimetic strategy is represented by the parasite's traits similar to those of the host ($\boldsymbol{x} \approx \boldsymbol{y}$), and the cryptic strategy is represented by the parasite's traits with small amount of chemicals ($\|\boldsymbol{y}\| \approx 0$). Here we focus on their chemical profile at the time of invading host colonies. We are not concerned about events after they invade successfully. For example, some parasites may use crypsis in the invading process, but change to mimesis after successfully invading the host colony, which is treated as a crypsis strategy in the following analysis.

According to empirical observations, we assume the rules of host acceptance as follows: [1] Ants accept other individuals whose blend of chemicals is similar to their own (van Zweden & d'Ettorre, 2010); and [2] ants tend to accept other individuals whose absolute amount of chemicals is small (Lenoir et al., 2001; Kilner & Langmore, 2011), because their own juveniles have small amounts of chemicals (Fielde, 1905; Morel et al., 1988; Van der Meer & Morel, 1998; Lenoir et al., 2001). Specifically, we assume that a host with chemical traits $\boldsymbol{x}$ will accept a parasite with chemical traits $\boldsymbol{y}$ with the following probability:

$$f(\boldsymbol{y}; \boldsymbol{x}, \beta_h) = \exp[-\beta_h(\|\boldsymbol{x} - \boldsymbol{y}\| + \|\boldsymbol{y}\| - \|\boldsymbol{x}\|)] \quad , \qquad (1)$$

where β_h indicates the accuracy of host recognition. This probability equals 1 along a line segment $\boldsymbol{y} = k\boldsymbol{x}$, where $0 \leq k \leq 1$, but it is smaller than 1 and it decreases as $\boldsymbol{y}$ diverges from the line segment (Figure. 2). When β_h is large, the value of function (1) decreases very quickly and has a sharp edge along the line segment, indicating that the host rejects individuals possessing traits slightly different from the host's. Hence, β_h represents the host's recognition accuracy.

Most parasitic and non-parasitic ants express chemical phenotypes similar to those of other colonies of the same species located nearby in the chemical profile space. Thus, ants are generally exposed to attacks by parasites of other species as well as by other colonies of conspecific ants through resource robbing (Ryti & Case, 1986; Gordon, 1991; Yamaguchi, 1995). Here we assume that parasites compete with each other, and that the competition incurs a large cost. In a similar manner as host ants, parasitic ants accept or reject invaders. Thus, the probability of a parasite with chemical traits $\boldsymbol{y}$ to accept a non-nestmate with chemical traits $\boldsymbol{z}$ is

$$f(\boldsymbol{y};\boldsymbol{z},\beta_p) = \exp[-\beta_p(\|\boldsymbol{y}-\boldsymbol{z}\| + \|\boldsymbol{z}\| - \|\boldsymbol{y}\|)] \quad , \qquad (2)$$

where β_p indicates the recognition accuracy of the parasite, which can differ from β_h, the recognition accuracy of the host.

Using Eqs. 1 and 2, we can calculate the fitness of a parasite with chemical traits $\boldsymbol{y}$ as

$$\ln W(\boldsymbol{y}) = \ln W_0 + a\sum_{i=1}^{n} f(\boldsymbol{x}_i;\boldsymbol{y},\beta_h) - b\sum_{j=1}^{m} f(\boldsymbol{y};\boldsymbol{z}_j,\beta_p) - c\|\boldsymbol{y}\| \ , (3)$$

In Eqs. 3, $\boldsymbol{x}_i$ represents the chemical traits of host i, $\boldsymbol{y}$ represents the focal parasite traits and $\boldsymbol{z}_j$ represents the parasite traits in other colonies around the focal parasite. Note that there can be multiple hosts differing in chemical profiles. n represents the number of host types and m represents the number of parasite colonies. Here, the number of host type means the number of host that have different chemical trait. The first term of the right-hand side of Eq. (3) is for the baseline fitness of parasites regardless of interaction with hosts and hydrocarbon production. The second term of equation (3) represents the benefit that is gained by successfully invading host colonies. If many host colonies are available, the parasite can acquire additional benefits. The third term reflects the risk of incorrectly accepting non-nestmates of the same species. The last term is the cost for production and maintenance of chemicals.

Mimetic parasite colonies can use host colonies in a different manner from each other, which makes them use chemical traits that differ from those of other colonies of the same parasite species. In contrast, cryptic parasites must use similar traits, which are near the origin of the chemical profile space. If many parasite colonies employ a cryptic strategy, they will have more conspecific colonies with chemical traits similar to themselves than a colony employing a mimetic strategy. Hence, a very strong intraspecific competition exerts a large effect among colonies with similar chemical traits, jeopardising cryptic parasites more strongly than mimic parasites.

Evolutionary dynamics in the chemical profile space

Here, we consider the evolutionary dynamics of the location of colonies in the chemical profile space. For simplicity, we consider a chemical profile with two dimensions in which axes are the first (y_1) and the second (y_2) components of ant chemicals. We divide the competition among parasites into two steps: the first step describes competition between colonies generated from the same colony, whilst the second step is the competition among colonies that survive the first step competition, which takes place in the whole area. The first step competition is severer than the second step not only because of the similarity of their traits, but also because they are spatially close to each other in the physical space. To represent the effect of physical proximity of colonies just produced from the same parental colony, we separated the competition among colonies in two steps. These dynamics are realised as follows:

The location of a colony in chemical profile space is characterised by the queen's chemical profile (Figure. 3-a). In the first step of competition, a colony of the parasite species produces new queens who are daughters of the queen. Their chemical profiles differ slightly from their mother's, due to mutations. We assume nine types of new queens. The trait values of a new queen are made by adding either minus 0.01 or plus 0.01 with equal probability to those of her mother (Figure. 3-b). The new queen with the highest fitness (calculated using Eq. 3) among them is assigned as the next queen and reorganises the colony's chemical traits with her own chemical profile (Figure. 3-c). We conduct this process for each colony of the parasite. As a consequence, each colony engages in an adaptive 'evolutionary random walk' on the chemical profile space.

The second step of competition takes place between all parasite colonies in the chemical profile space. We calculate the fitness of each colony and the fitness value averaged over all colonies. We remove the colonies with fitness less than 80% of the mean fitness. To maintain the number of colonies in the area, we duplicate the colonies with high fitness (Figure. 3-d). The colonies that are duplicated are selected from those with the highest fitness among the colonies in the population. We chose the number of colonies duplicated equal to the number of colonies removed (i.e. the colonies with low fitness). According to numerical analyses for a range of parameters, in most cases, the fitness of the colonies allowed to duplicate is more than 1.1-times larger than the mean fitness of all colonies. Here we assume that each new colony has chemical traits slightly different from the parental colony by mutation. The values of an offspring colony are made by adding minus 0.01 or plus 0.01 (with 50% chance) to the values of the parental colony.

In the initial population, we placed 100 parasites colonies (m=100) in two-dimensional chemical profile space and conducted the evolutionary procedure described above. We chose the value of initial traits (y_1 and y_2) of parasites randomly between 0 and 1 with uniform probability distribution. Traits of each hosts (x_1 and x_2) are chosen randomly between 0.2 and 1 with uniform probability distribution. The fitness given by Eq. 3 depends on the distances of traits from other conspecific colonies and from host colonies. Therefore, the fitness landscape changes as traits of the parasites change, generating frequency dependent natural selection. In the end, all colonies ceased to show large conspicuous changes, which we regard as the evolutionary equilibrium. In this way, we calculated evolutionary outcomes and its parameter dependence numerically. We found that parameters a, b, n, m, and β_h had large effects to outcomes, and other parameters had smaller effect than these.

Evolutionary outcomes

Figure 4-a illustrates an evolutionary outcome. Here we operationally define parasites' strategy according to their chemical traits as follows: (i) cryptic, if the magnitude of the parasite traits' vector ($||\boldsymbol{y}||$) is $\leq$ 0.4; (ii) intermeditate, if $0.4 < ||\boldsymbol{y}|| < 0.8$; and (iii) mimetic, if $||\boldsymbol{y}||$ is $\geq$ 0.8. Since there are no criteria for real ants to distinguish two strategies, we use above values operationally.

At evolutionary endpoints, parasites are cryptic when the strength of intraspecific competition (b) is small and when the number of host types (n) is large; and parasites are mimetic when b is large and the number of host types is small. These results can be interpreted as follows: Parasites employing a cryptic strategy are likely to be accepted by hosts of more diverse types than mimetic parasites. On the other hand, they suffer from severe competition among themselves more than mimetic parasites.

Parameter m (the number of parasites) has a similar effect to b, because the loss by competition is determined by b times the number of competitors. Parasites evolved to be mimic if m is large, and evolved to be cryptic if m is small. At the boundary between the parameter region for mimicry and that for crypsis, there was a narrow region with an intermediate strategy evolved, but we never observed the coexistence of multiple types (see below for more details).

Figure. 4-b illustrates the evolutionary outcome when β_h, host recognition accuracy is much larger than that shown in Figure. 4-a. As the host's recognition accuracy β_h becomes larger, the cryptic strategy (rather than mimic strategy) evolves even for fewer host types. This can be interpreted as follows: When host recognition accuracy is limited, parasites with chemical profiles different from the host can be accepted. In such cases, a parasite mimicking one host colony (with a chemical profile very similar to a particular host) will be accepted also by other host colonies even if chemical profiles of the host colonies are slightly different from that of the parasite. This is the reason why mimic strategy works well under limited host recognition accuracy. In contrast, if the host's recognition accuracy is very high, a parasite with a profile close to a host colony will be rejected by the other host colonies, which makes the mimic strategy less profitable.

We carefully examined the evolutionary outcome near the boundary between the parameter region for mimicry and the region for crypsis with different *b* values. In particular, we examined the model with *b* changing by small steps (0.01-fold difference) near the boundary between two regions. Figure. 5 illustrates the evolutionary endpoints with different *b* value. Horizontal axis represents *b* and vertical axis represents the magnitude of chemical traits of parasites ($||\boldsymbol{y}||$). We never observed the coexistence of two strategies in the same population. However, we observed the evolution of an intermediate strategy in a very small parameter range.

Parameter *a* also affects the result strongly. Figure. 6 illustrates the evolutionary outcome with different *a* and *b*. Horizontal axis represents the intensity of competition, *b*, and vertical axis represents the benefit from host, *a*. Parasites employing cryptic strategy suffer from more severe competition among themselves, but they can exploit more diverse host types than mimic parasites. Therefore, cryptic strategy tends to evolve when the benefit from a host (*a*) is large. From this figure, we conclude that the successful strategy is decided by the balance between the benefit from host, *a*, and the loss by competition among parasites, *b*.

Parameter *c* changes the results quantitatively, although it has smaller impact than other parameters mentioned above. When the cost of chemicals, *c,* becomes larger, the boundary between mimic and cryptic in Figure.4 shifts toward right, implying that the parameter region for cryptic strategy to evolve becomes larger. The reason is that parasites which have no chemicals are favored when the cost of chemicals is large.

Discussion

In this paper, we analysed the conditions under which the chemical strategies of crypsis and mimicry evolve in parasitic ants that invade colonies of host ants. We assumed that parasitic ants possess their own colonies and that parasitic and non-parasitic ants prevent invaders from entering their own nest by detecting chemical cues. We evaluated the chemical strategies that occur at the evolutionary end point and identified factors that strongly influence the optimal strategy as follows:

i) *Competition intensity and benefit from host*

First, the model predicts that a cryptic strategy evolves when competition among parasite colonies is mild and parasites can obtain a large benefit from the host, whereas a mimetic strategy evolves when competition is intense and benefit from host is small. Cryptic parasites do not have strong chemical components. On the chemical profile space, they are represented by points near the origin. Since they get close to each other, they are likely to engage in competition among themselves. The cryptic parasites experience stronger competition among themselves than mimetic parasites, and they are defeated by mimetic parasites when competition is intense. In contrast, when competition is mild, cryptic parasites enjoy larger benefits, because they can invade more host colonies than mimetic parasites.

Our theory predicts that the chemical strategy should correspond to the strength of competition b and the size of benefit from host a. Some ant species kill non-nestmates on contact (Holldobler, 1976b, 1983; Yamaguchi, 1995), while others exclude conspecific invaders through ritualised combat (Ettershank & Ettershank, 1982). Hence the strength of competition can be guessed for some species. However, at this moment, there is no report available which measures the size of the benefit from host quantitatively. Hence, although ant chemical strategies are known for many species (Akino, 2008), we cannot test the theory because no study was done on quantitative measurements of both *a* and *b* for the same species.

ii) *Number of host types*

Second, the model predicts that a cryptic strategy is more likely to evolve when there are many host types, whereas a mimetic strategy is likely to evolve under the opposite conditions. The diversity of ant colonies' phenotypes may vary between habitats and between local populations (e.g. Nash et. al., 2008). To test the model's prediction, we need to know the relationship between diversity of host colonies and chemical strategies of parasites.

iii) *Recognition accuracy of the host*

Third, the model predicts that cryptic strategies are more likely to evolve if host recognition accuracy is high. Nestmate recognition accuracy and intraspecific aggression vary greatly among species (e.g. Cini et al., 2009; Furst et al 2012; Cappa et al 2014). Cini et al. (2009) reported a quantitative recognition threshold for paper wasp *Polistes dominulus*. The wasp is a social insect, like most ants, and it recognises nestmates using hydrocarbons on the body; and Cappa et al. (2014) measured the recognition threshold in honeybee *Apis mellifera* quantitatively. Furst (2012) reported the relationship between aggression level and distance of chemicals. However, to test our predictions, we need to focus not only on chemical distances but also on the types of chemical strategies (crypsis or mimesis).

An important finding of the present study is that the evolution of mimetic and cryptic strategies can be explained by considering the effect of intraspecific competition among colonies. Intraspecific competition occurs among ants (Hölldobler, 1976, 1983; Yamaguchi, 1995; Ettershank & Ettershank, 1982, Cronin et. al., 2012, Jandt et. al., 2015), although the relationship between their competitive behaviours and chemical strategies is unknown. Our model predicts that the strength of competition affects the chemical strategy of parasites -- a mimic strategy is likely to evolve when parasite colonies engage in strong competition with each other. This remains to be tested empirically.

iv) *Difficulty of Coexistence of Cryptic and Mimic Strategies*

In our model, there was no instance of coexistence of the cryptic strategy with the mimic strategy. In addition, we never observed evolutionary bistability. The outcome was invariably one or the other in all the 10 runs with different initial conditions. This theoretical result is consistent with findings that most parasitic ants are cryptic or mimic, depending on species. However, the model also allows subpopulations of the same species living in different habitats to take different chemical strategies. In fact, in *Protomognathus americanus,* individuals from some colonies has strong odors similar to one host species, whilst individuals from other colonies have weak odors, which is not very similar to the host's odors, and that they live in different habitats (Brandt et al., 2005). Former individuals exploit one host species and latter individuals exploit multiple host species. The theoretical results of the model suggest that colonies employing a cryptic strategy live in habitats with numerous host species, while colonies employing a mimic strategy live in an environment with a few host species. This predicted pattern is consistent with a field study of *P. americanus* (Brandt et al., 2005).

At the boundary between the parameter region for mimicry and the one for crypsis, there is a narrow region in which an intermediate strategy evolved. In ants, it is difficult to discuss an intermediate strategy because there are no quantitative criteria between cryptic and mimic strategy. However, it is quite interesting to search for a case with an intermediate strategy, which may be possible when a subtle balance holds between benefit from host and loss by competition among parasites.

v) *Possible Extrapolation to Other Species*

In this paper, we developed a model targeting parasitic ants, but we may extend the model to chemical strategies of other species that attack colonies of social insects. An obvious extension is for non-ant species of hymenopteran social insects, which adopt chemical odours to distinguish nestmates from non-nestmates. Among them, particularly social wasps, parasite species invade other colonies and steal food and other resources (Sledge et al., 2001). These social wasp species recognise individuals from other colonies using chemical signals, and mimic and cryptic species exist among parasites, similar to ants (Cini et al., 2009). We conjecture that the same theory applies to parasitic wasps that attack other social wasps.

The model studied in this paper may be applicable to parasites of colonies of social insects, even if parasites themselves are not social insects. For example, the silverfish *Malayatelura ponerophila* is a specialized parasite often observed in ant colonies. Silverfish have very little cuticular hydrocarbons, which help them invade ant colonies (von Beeren et al., 2011). Our model considers this a cryptic strategy. Silverfish are not social, but live without forming colonies and do not engage in inter-colonial competition. Therefore, *b* (strength of competition among colonies) in our model should approach zero. The model then predicts that silverfish should adopt a cryptic, rather than a mimic strategy. Similarly, blue butterfly *Eumaeus atala* catapillars and ant spiders *Mirmanachne* spp. are accepted in ant colonies, and both adopt a cryptic strategy (Bowers & Larin, 1989; Elgar & Allan, 2004), which is consistent with our model. These results indicate that the magnitude of inter-colony competition is important for the evolution of the mimicry of chemical profiles.

Future developments

In the present study, we considered the traits of host colonies as fixed. However, host traits may coevolve with those of parasites. Many studies focus on the coevolution of hosts and mimetic parasites. For example, Gavrilets (1997) found that host traits evolve in the opposite direction from parasite traits, resulting in an evolutionary arms race. However, few studies analyse the evolution of hosts in response to cryptic parasites. Kilner and Langmore (2011) suggest that host colonies exposed to cryptic parasitism may decrease their chemical recognition cues and evolve to detect their cryptic parasites. Thus, a question for future theoretical studies is the evolutionary direction of host colonies that are simultaneously exposed to mimetic and cryptic parasites.

For simplicity, we assumed two-dimensional chemical traits. However, in reality, the number of recognition cues may be greater than two and may vary among species. In a review article, Martin (2009) compared cuticular hydrocarbon profiles of 78 ants, some ants have 20 or more types of hydrocarbons, other ants have less than 5 types. A larger number of recognition cues should make it easier to distinguish parasites from other colonies, weakening the strength of competition. This suggests that cryptic parasites may receive more benefit when there are many chemical traits than when there are only two chemical traits.

In reality, life cycle and chemical strategy of ants are more complex than assumed in the model. In the present study, we focused on the chemical strategy when a parasite invades host colonies, and we classified the strategy into two: cryptic and mimic. However, some parasites adopt cryptic strategy before invasion and mimic strategy after invasion by gaining and maintaining the chemical profile by contacting host ants (Nehring et al., 2015). In future, the model should be constructed by considering this strategy and it will be helpful to verify the predictions by experimental studies.

Mimicry system is common and has been the subject of numerous theoretical studies. In contrast, the strategies of mimicry are diverse, and their evolutionary outcomes may critically depend on the nature of sensor and recognition systems. Further theoretical studies of possible outcomes of evolution of different systems are required to understand the evolution of chemical mimicry and chemical crypsis.

References

Akino, T. (2008). Chemical strategies to deal with ants: a review of mimicry, camouflage, propaganda, and phytomimesis by ants (Hymenoptera: Formicidae) and other arthropods. *Myrmecological News, 11*, 173-181.

Akino, T., Terayama, M., Wakamura, S., & Yamaoka, R. (2002). Intraspecific variation of cuticular hydrocarbon composition in Formica japonica Motschoulsky (Hymenoptera: Formicidae). *Zoological science, 19*(10), 1155-1165.

Akino, T., Yamamura, K., Wakamura, S., & Yamaoka, R. (2004). Direct behavioral evidence for hydrocarbons as nestmate recognition cues in Formica japonica (Hymenoptera: Formicidae). *Applied Entomology and Zoology, 39*(3), 381-387.

Bowers, M. D., & Larin, Z. (1989). Acquired chemical defense in the lycaenid butterfly, Eumaeus atala. *Journal of Chemical Ecology, 15*(4), 1133-1146.

Brandt, M., Heinze, J., Schmitt, T., & Foitzik, S. (2005). A chemical level in the coevolutionary arms race between an ant social parasite and its hosts. *Journal of Evolutionary Biology, 18*(3), 576-586. doi:10.1111/j.1420-9101.2004.00867.x

Breed, M. D., Cook, C., & Krasnec, M. O. (2012). Cleptobiosis in social insects. *Psyche: A Journal of Entomology, 2012*(2012), 1-7.

Cappa, F., Bruschini, C., Cipollini, M., Pieraccini, G., & Cervo, R. (2014). Sensing the intruder: a quantitative threshold for recognition cues perception in honeybees. *Naturwissenschaften, 101*(2), 149-152. doi:10.1007/s00114-013-1135-1

Cronin, A. L., Fédérici, P., Doums, C., & Monnin, T. (2012). The influence of intraspecific competition on resource allocation during dependent colony foundation in a social insect. *Oecologia, 168*(2), 361-369.

Cheney, K. L. (2012). Cleaner wrasse mimics inflict higher costs on their models when they are more aggressive towards signal receivers. *Biology Letters, 8*(1), 10-12.

Cini, A., Gioli, L., & Cervo, R. (2009). A quantitative threshold for nest-mate recognition in a paper social wasp. *Biology Letters, 5*(4), 459-461.

Dettner, K., & Liepert, C. (1994). CHEMICAL MIMICRY AND CAMOUFLAGE. *Annual Review of Entomology, 39*, 129-154.

Elgar, M. A., & Allan, R. A. (2004). Predatory spider mimics acquire colony-specific cuticular hydrocarbons from their ant model prey. *Naturwissenschaften, 91*(3), 143-147.

Ettershank, G., & Ettershank, J. (1982). Ritualised fighting in the meat ant Iridomyrmex purpureus (Smith)(Hymenoptera: Formicidae). *Australian Journal of Entomology, 21*(2), 97-102..

Fielde, A. M. (1905). The progressive odor of ants. *The Biological Bulletin, 10*(1), 1-16.

Fürst, M. A., Durey, M., & Nash, D. R. (2012). Testing the adjustable threshold model for intruder recognition on Myrmica ants in the context of a social parasite. *Proc Biol Sci*, 279(1728), 516-522.

Gavrilets, S. (1997). Coevolutionary chase in exploiter–victim systems with polygenic characters. *Journal of Theoretical Biology, 186*(4), 527-534.

Gordon, D. M. (1991). Behavioral flexibility and the foraging ecology of seed-eating ants. *American Naturalist*, 379-411.

Hölldobler, B. (1976). Recruitment behavior, home range orientation and territoriality in harvester ants, Pogonomyrmex. *Behavioral Ecology and Sociobiology*, *1*(1), 3-44.

Hölldobler, B. (1983). Territorial behavior in the green tree ant (Oecophylla smaragdina). *Biotropica*, 241-250.

Howard, R. W., & Blomquist, G. J. (2005). Ecological, behavioral, and biochemical aspects of insect hydrocarbons*. *Annu. Rev. Entomol., 50*, 371-393.

Huang, J.-N., Cheng, R.-C., Li, D., & Tso, I.-M. (2010). Salticid predation as one potential driving force of ant mimicry in jumping spiders. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*, 1356-1364.

Jandt, J. M., Hunt, E. M., & McGlynn, T. P. (2015). Intraspecific Food‐Robbing and Neighborhood Competition: Consequences for Anti‐Robber Vigilance and Colony Productivity. *Biotropica, 47*(4), 491-496.

Kilner, R. M., & Langmore, N. E. (2011). Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. *Biol Rev Camb Philos Soc, 86*(4), 836-852. doi:10.1111/j.1469-185X.2010.00173.x

Langmore, N., Stevens, M., Maurer, G., & Kilner, R. (2009). Are dark cuckoo eggs cryptic in host nests? *Animal Behaviour, 78*(2), 461-468.

Larsen, J., Fouks, B., Bos, N., d’Ettorre, P., & Nehring, V. (2014). Variation in nestmate recognition ability among polymorphic leaf-cutting ant workers. *Journal of insect physiology, 70*, 59-66.

Lenoir, A., D'Ettorre, P., Errard, C., & Hefetz, A. (2001). Chemical ecology and social parasitism in ants. *Annual Review of Entomology, 46*, 573-599. doi:10.1146/annurev.ento.46.1.573

Lenoir, A., Fresneau, D., Errard, C., & Hefetz, A. (1999). Individuality and colonial identity in ants: the emergence of the social representation concept *Information processing in social insects* (Ed. Dertain C., Deneubourg J.L. and Pasteels J.M.), pp. 219-237, Birkhauser Verlag, Basel

Lhomme, P., Ayasse, M., Valterova, I., Lecocq, T., & Rasmont, P. (2012). Born in an Alien Nest : How Do Social Parasite Male Offspring Escape from Host Aggression? *PLoS One, 7*(9), e43053. doi:10.1371/journal.pone.0043053

Liefke, C., Hölldobler, B., & Maschwitz, U. (2001). Recruitment behavior in the ant genus Polyrhachis (Hymenoptera, Formicidae). *Journal of Insect Behavior, 14*(5), 637-657.

Marchant, S. (1972). Evolution of the genus Chrysococcyx. *Ibis, 114*(2), 219-233.

Martin, S. J., Takahashi, J.-i., Ono, M., & Drijfhout, F. P. (2008). Is the social parasite Vespa dybowskii using chemical transparency to get her eggs accepted? *Journal of Insect Physiology, 54*(4), 700-707.

Martin, S., & Drijfhout, F. (2009). A review of ant cuticular hydrocarbons. *Journal of chemical ecology*, *35*(10), 1151.

Maschwitz, U., Dorow, W., Buschinger, A., & Kalytta, G. (2000). Social parasitism involving ants of different subfamilies: Polyrhachis lama (Formicinae) an obligatory inquiline of Diacamma sp.(Ponerinae) in Java. *Insectes Sociaux, 47*(1), 27-35.

Maschwitz, U., Go, C., Kaufmann, E., & Buschinger, A. (2004). A unique strategy of host colony exploitation in a parasitic ant: workers of Polyrhachis lama rear their brood in neighbouring host nests. *Naturwissenschaften, 91*(1), 40-43.

Morel, L., Vander Meer, R. K., & Lavine, B. K. (1988). Ontogeny of nestmate recognition cues in the red carpenter ant (Camponotus floridanus). *Behavioral Ecology and Sociobiology, 22*(3), 175-183.

Mori, n. A., D'Ettorre, P., & Le Moli, F. (1995). Host nest usurpation and colony foundation in the European amazon ant, Polyergus rufescens Latr.(Hymenoptera: Formicidae). *Insectes Sociaux, 42*(3), 279-286.

Nash, D. R., Als, T. D., Maile, R., Jones, G. R., & Boomsma, J. J. (2008). A mosaic of chemical coevolution in a large blue butterfly. *Science*, 319, 88-90.

Nehring, V., Dani, F.R., Turillazzi, S., Boomsma, J. J., & D'Ettorre, P. (2015). "Integration strategies of a leaf-cutting ant social parasite." *Animal Behaviour 108*: 55-65.

Ozaki, M., & Wada-Katsumata, A. (2010). Perception and olfaction of cuticular compounds. *Insect hydrocarbons: biology, biochemistry and chemical ecology* (Ed. by Blomquist G.J. and Bagneres A-G.)*, 10*, pp. 207-221, Cambridge University Press, Cambridge..

Pasteur, G. (1982). A classification review of mimicry systems. *Annual Review of Ecology and Systematics, 13*, 169-199.

Perfecto, I., & Vandermeer, J. (1993). Cleptobiosis in the antEctatomma ruidum in Nicaragua. *Insectes Sociaux, 40*(3), 295-299.

Rodríguez-Gironés, M. A., & Lotem, A. (1999). How to detect a cuckoo egg: a signal-detection theory model for recognition and learning. *The American Naturalist, 153*(6), 633-648.

Ryti, R. T., & Case, T. J. (1988). Field experiments on desert ants: testing for competition between colonies. *Ecology, 69*(6), 1993-2003.

Sasaki, A. (2000). Host-parasite coevolution in a multilocus gene-for-gene system. *Proceedings of the Royal Society of London B: Biological Sciences, 267*(1458), 2183-2188.

Saul-Gershenz, L. S., & Millar, J. G. (2006). Phoretic nest parasites use sexual deception to obtain transport to their host's nest. *Proceedings of the National Academy of Sciences of the United States of America, 103*(38), 14039-14044. doi:10.1073/pnas.0603901103

Singer, T. L. (1998). Roles of Hydrocarbons in the Recognition Systems of Insects1. *American Zoologist, 38*(2), 394-405.

Sledge, M. F., Dani, F. R., Cervo, R., Dapporto, L., & Turillazzi, S. (2001). Recognition of social parasites as nest-mates: adoption of colony-specific host cuticular odours by the paper wasp parasite Polistes sulcifer. *Proceedings of the Royal Society of London B: Biological Sciences, 268*(1482), 2253-2260..

Stevens, M. (2013). *Sensory ecology, behaviour, and evolution*: Oxford University Press.

Sumner, S., Nash, D. R., & Boomsma, J. J. (2003). The adaptive significance of inquiline parasite workers. *Proceedings of the Royal Society of London B: Biological Sciences, 270*(1521), 1315-1322.

Topoff, H., & Zimmerli, E. (1993). Colony takeover by a socially parasitic ant, Polyergus breviceps: the role of chemicals obtained during host-queen killing. *Animal Behaviour, 46*(3), 479-486.

van Zweden, J. S., & d'Ettorre, P. (2010). Nestmate recognition in social insects and the role of hydrocarbons. *Insect hydrocarbons: biology, biochemistry and chemical ecology* (Ed. by Blomquist G.J. and Bagneres A-G.)*, 11*, pp.222-243, Cambridge University Press, Cambridge.

Vander Meer, R. K., & Morel, L. (1998). Nestmate recognition in ants. *Pheromone communication in social insects*, 79-103.

von Beeren, C. v., Schulz, S., Hashim, R., & Witte, V. (2011). Acquisition of chemical recognition cues facilitates integration into ant societies. *BMC Ecology, 11*, 30. doi:10.1186/1472-6785-11-30

Ward, S. (1996). A new workerless social parasite in the ant genus Pseudomyrmex (Hymenoptera: Formicidae), with a discussion of the origin of social parasitism in ants. *Systematic Entomology, 21*(3), 253-263.

Witte, V., Lehmann, L., Lustig, A., & Maschwitz, U. (2009). Polyrhachis lama, a parasitic ant with an exceptional mode of social integration. *Insectes Sociaux, 56*(3), 301-307.

Yamaguchi, T. (1995). Intraspecific competition through food robbing in the harvester ant, Messor aciculatus (Fr. Smith), and its consequences on colony survival. *Insectes Sociaux, 42*(1), 89-101.

Figures

Figure 1

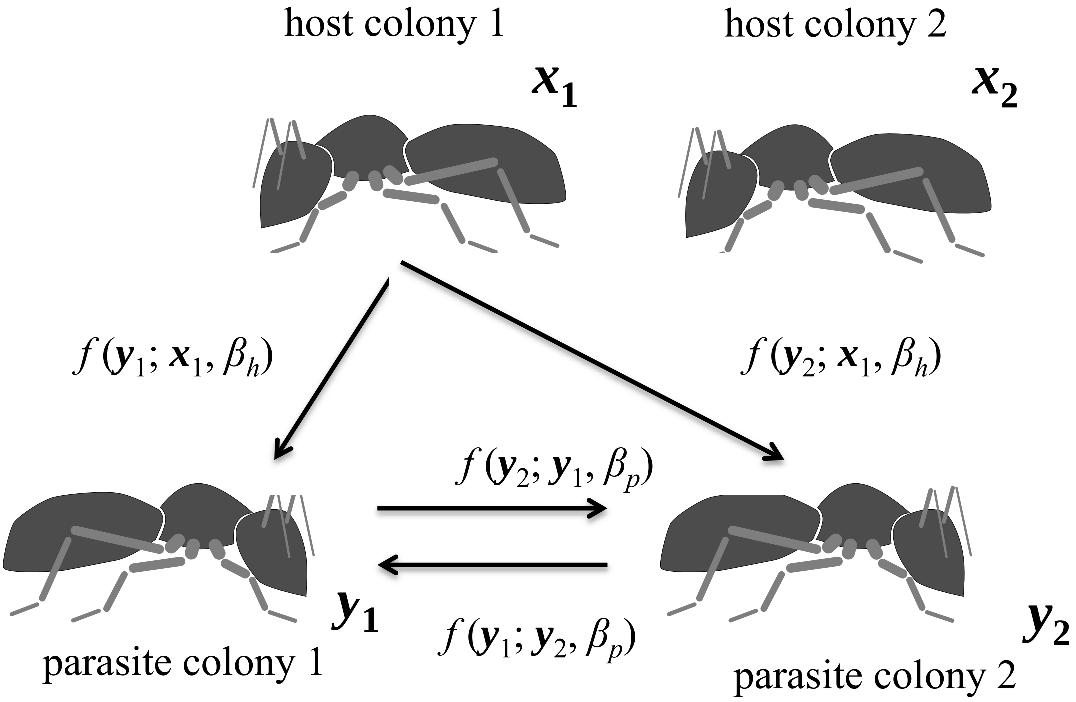


Figure 1. Schematic diagram of the model. We consider the situation where there are multiple host and parasitic ant colonies. Parasitic ants invade the host colonies and steal their resources. Host ants distinguish invaders from their nestmates and decide whether to accept them as described by function *f*. Parasitic ants compete with each other by stealing resources, and they also distinguish invaders from their nestmates.

Figure 2

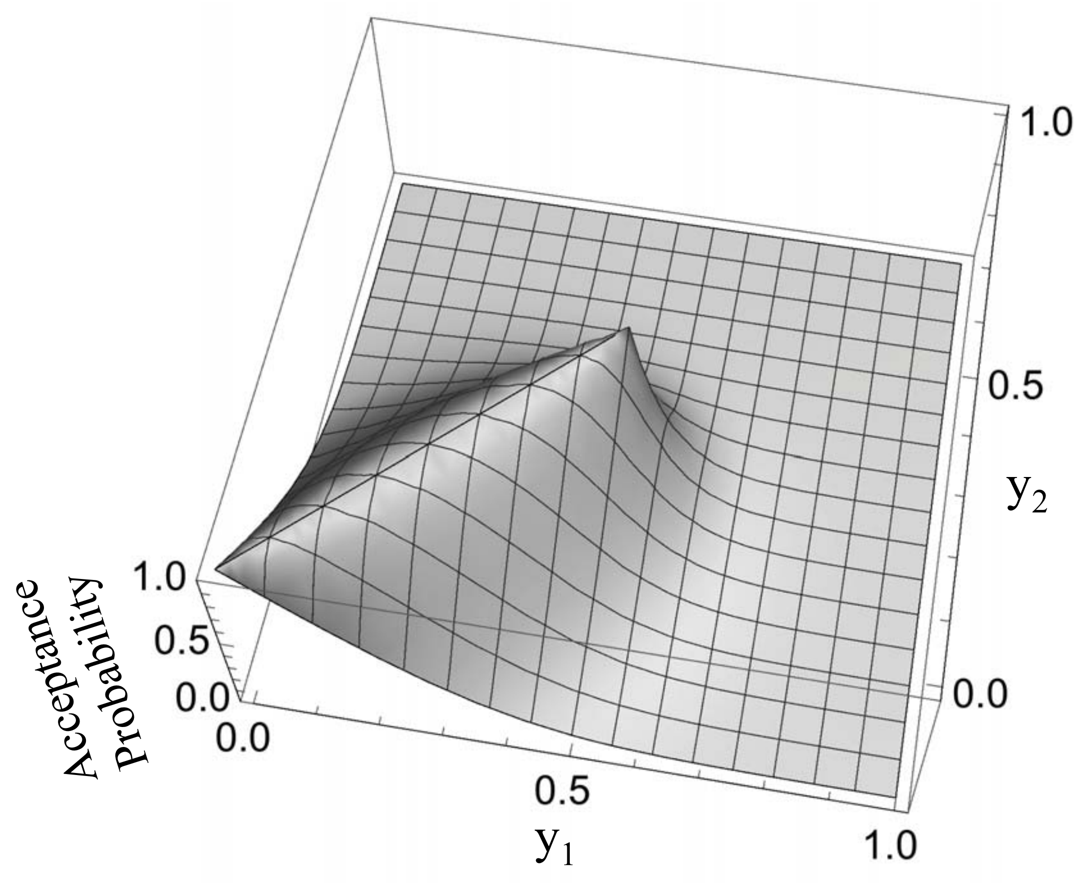


Figure 2. Probability for an ant's colony to accept a parasite individual. Two axes indicate two chemical traits of a parasite (y_1 and y_2, respectively). The height indicates the acceptance probability (i.e. the probability for an invader to be accepted by the host ants). The host ants' traits are (0.5, 0.5). If the parasites' traits are larger than the hosts' traits, they will be rejected, i.e. the acceptance probability is small. However, if the parasites' traits are weaker than the hosts' traits, they will be accepted if the proportion of chemical components is similar to the hosts'. Parameters are $\boldsymbol{x} = (0.5, 0.5)$ and $\beta_h = 5$.

Figure 3

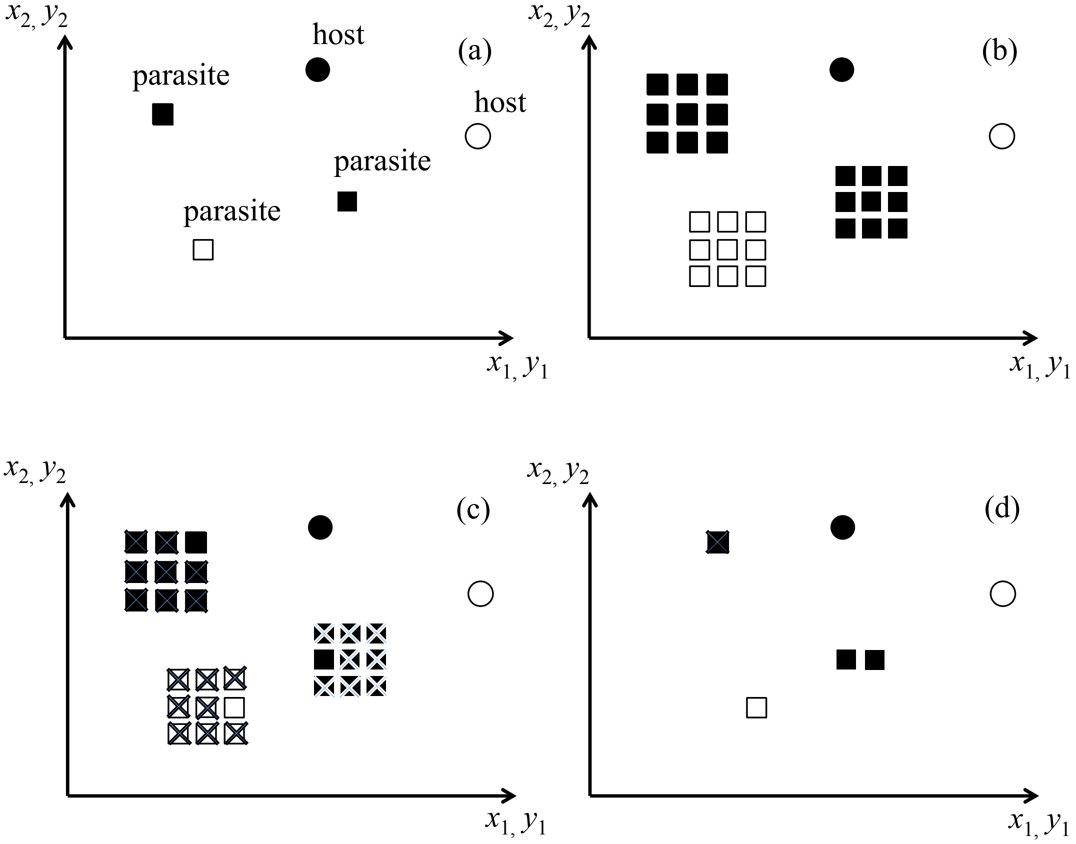


Figure 3. Schematic illustrations of the simulation. Horizontal axis represents the first component of the two chemicals (x_1 or y_1) and vertical axis represents the second component (x_2 or y_2). (a) There are two colonies of hosts and three colonies of parasites in chemical profile space. (b) New queens are produced in each colony of parasitic species. Their traits are slightly different from mother's traits. (c) Only one colony wins the competition among daughter colonies from a mother queen and all the others are eliminated in the first step competition. (d) Those colonies that survive the first-step competition engage in the second-step competition. Colonies which have the high fitness multiply, and colonies which have low fitness go extinct.

Figure 4

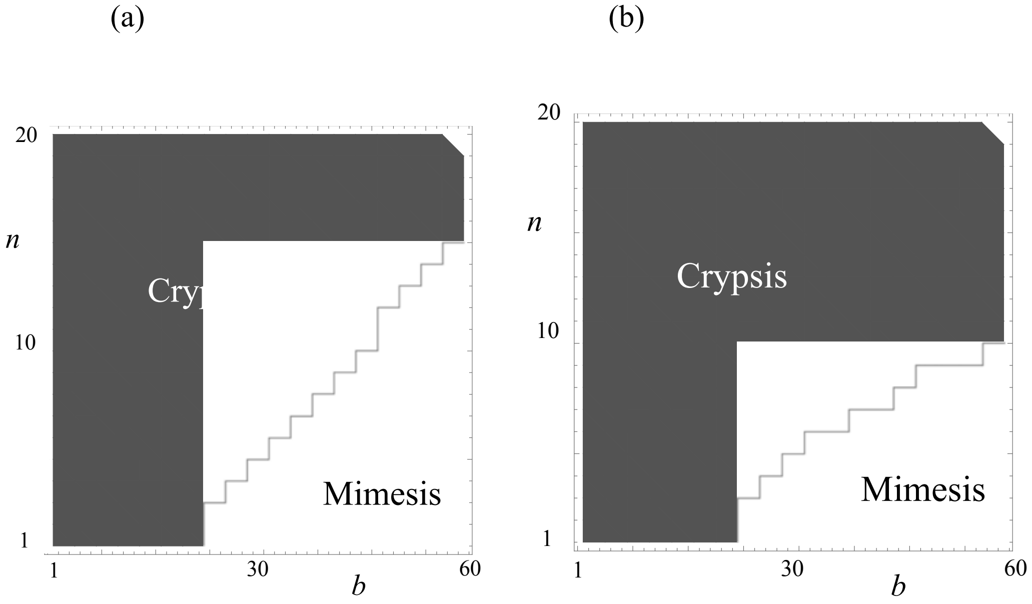


Figure 4. Relative abundance of the two strategies for different parameter values where host recognition accuracy was (a) low ($\beta_h = 2$) or (b) high ($\beta_h = 20$). Horizontal axis represents the strength of competition among parasites, b, and vertical axis represents the number of host types, n. The black region indicates cases where all colonies adopted a cryptic strategy, and the white region represents cases in which all colonies employed a mimetic strategy. Parameters: $a = 80$, $c = 1$, $m = 100$ and $\beta_p = 10$.

Figure 5

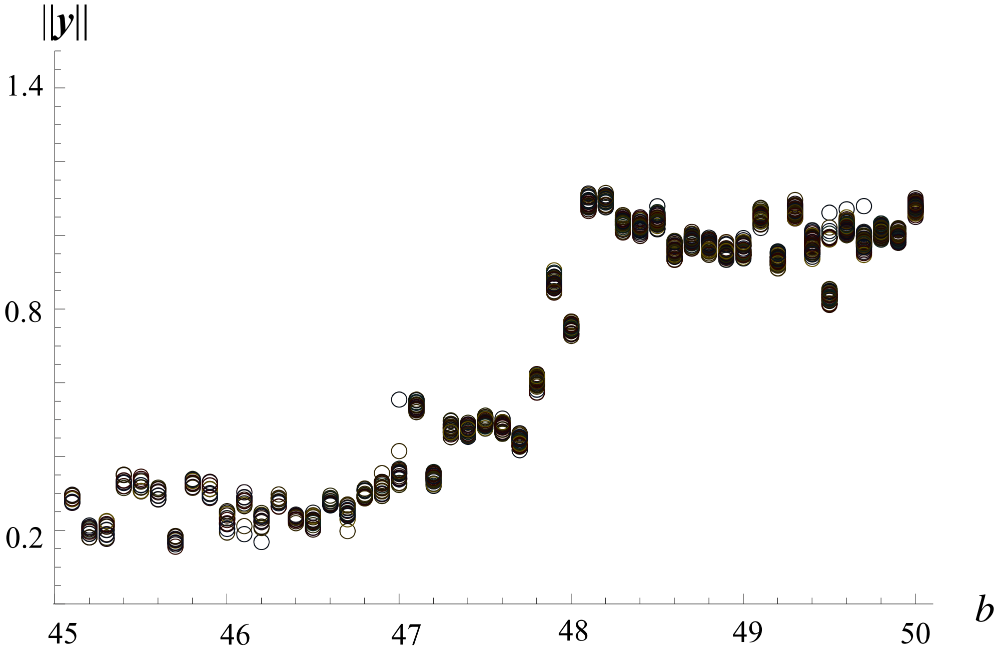


Figure 5. Magnitude of parasites' trait to evolve for different *b* values. Horizontal axis represents the strength of competition among parasites, *b*, and vertical axis represents the magnitude of chemical traits of parasites. Each circle of this figure indicates the magnitude of traits ($||\boldsymbol{y}||$) of each colony. The quantity is the magnitude of the chemical traits, indicating the distance from the origin in chemical profile space. Parameters are: a=80, c=1, n=10, m=100, β_p=10, and β_h=2.

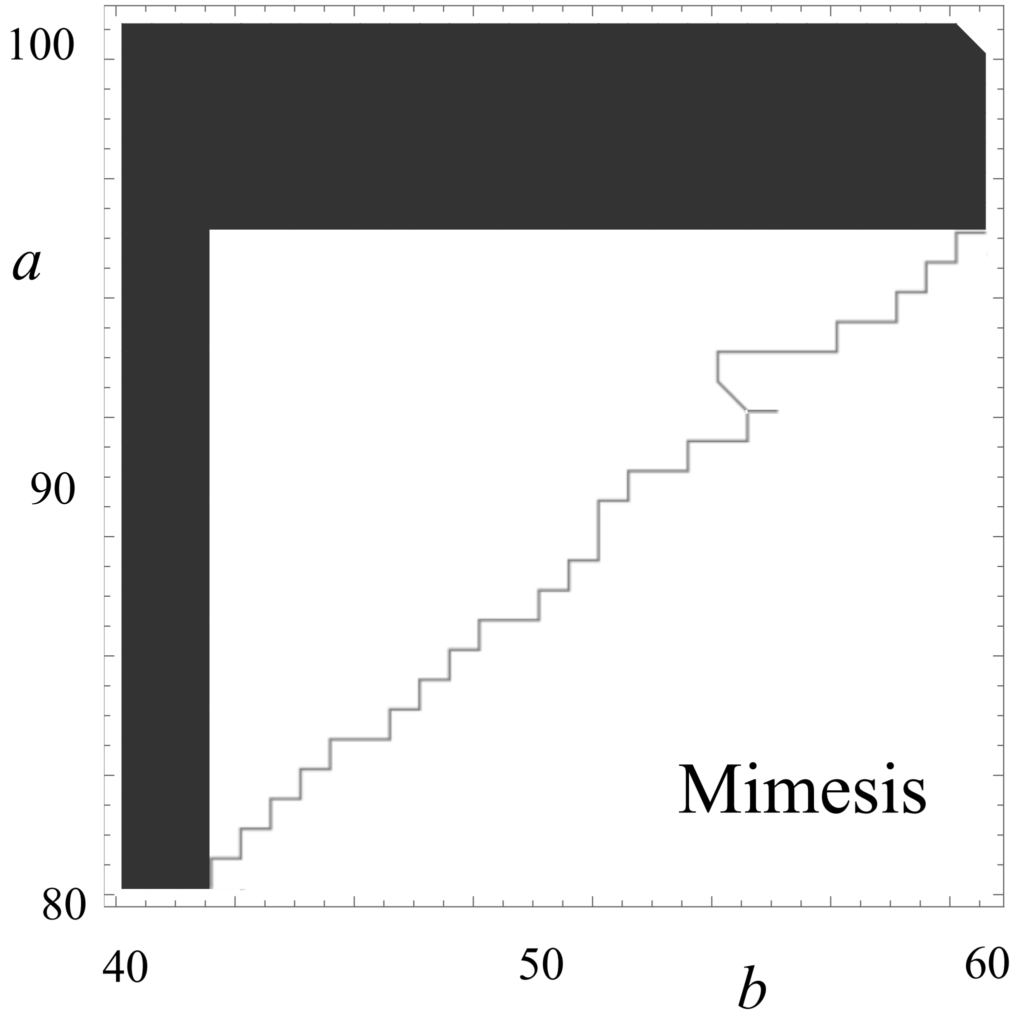


Figure 6. Contour plot of the parasites' strategy in the evolutionary endpoint. Horizontal axis represents the strength of competition among parasites, *b*, and vertical axis represents benefit from host, *a*. The black region indicates cases where all colonies adopted a cryptic strategy, and the white region represents cases in which all colonies employed a mimetic strategy. Parameters are: c=1, n=10, m=100, β_p=10, β_h=2

Chapter 2

When faster moving animals have better visual ability?

-- computational study of Leuckart’s law

The study of this chapter, done in collaboration with Dr. Yoh Iwas, was published in

Evolutionary Ecology Research (16, 8, pp.649-661) in 2015

Introduction

Animals obtain information regarding their physical and social environments through diverse sensory organs, receiving visual, auditory, tactile, and chemical signals. The size, position, and ability of sensory organs likely evolved based on their costs and benefits to the organism (Walls, 1942; Eisthen, 1977; Hughes, 1977; Fay and Popper, 2000). Eyes are sensory organs for light, and almost all animals are equipped with eyes or organs with a similar function. The size of eyes is affected by many factors, such as body size (Schultz, 1940; Kiltie, 2000; Howland et al., 2004; Burton, 2008), activity pattern (Kay and Kirk, 2000; Garamszegi et al., 2002; Hall and Ross, 2006; Kirk, 2006; Werner and Seifan, 2006; Hall, 2008), and diet (Garamszegi et al., 2002; Lisney and Collin, 2007).

Leuckart (1876) proposed that swifter animals tend to have larger eyes compared to slower-moving species. Leuckart's Law predicts a positive correlation between locomotive speed and eye size of animals if other aspects of their lives are equal (Leuckart, 1876; Walls, 1942; Hughes, 1977). Eyesight involves two different features: sensitivity and resolution. Sensitivity allows nocturnal vision, and a high sensitivity allows animals to see surroundings under limited light conditions. In contrast, resolution refers to the precision of eyes, and animals with eyes capable of high resolution can see surroundings clearly and in fine detail. Both sensitivity and resolution are improved with larger eyes (Land and Nilsson, 2012).

Swift animals need to recognize surrounding objects while they are still far away, so they need eyes with high resolution that allow them to see distant objects clearly (Hughes, 1997; Heard-Booth and Kirk, 2012). Higher resolution is achieved by larger eyes, so Leuckart's proposal of a positive correlation between locomotive speed and eye size is a plausible hypothesis. However, because of the difficulty of measuring the movement speed of animals, Leuckart's Law has not been empirically examined for the more than 100 years since its proposal. Brooks et al. (1999) studied the relationship between eye mass and flight speed predicted by fluid mechanics in 104 flying bird species and confirmed a positive correlation between the two variables. They also found that eye mass was smaller among flightless birds than among flying birds, after controlling for body mass. Kirk (2006) demonstrated that patas monkeys, which move quickly, have a relatively large eye size among primates.

However, Hall and Heesy (2011) examined axial eye diameter and flight speed in 88 avian species, representing the first test of Leuckart's Law based on direct measurements of flight speed (earlier studies only estimated flight speed). They were unable to detect a correlation in birds between eye size and movement speed. Furthermore, they observed a negative correlation between relative eye size and movement speed, which appears to contradict Leuckart's Law (Hall and Heesy, 2011). They concluded that variation in bird eye size is mainly driven by factors other than movement speed. Heard-Booth and Kirk (2012) examined axial eye diameter and running speed in 50 species from 10 mammalian orders. They found a significantly positive correlation between absolute eye size and running speed in mammals. Moreover, the relationship between eye size and running speed was still significant when the effects of body mass and phylogeny were statistically controlled (Heard-Booth and Kirk, 2012). Thus, these two comparative studies, conducted using different taxonomic groups, reached different conclusions.

Here, I examine the conditions under which Leuckart's Law holds, i.e., when eye size and movement speed are positively correlated, and when the inclination of the linear regression between moving speed and eye size increases that means Leuckart's Law holds conspicuously. I conducted computer simulations of an animal moving on a plane that contains many food items as well as obstacles. The animal moved at a constant speed but changed its directional angle when it recognized food items or obstacles. By considering the number of food items consumed, the number of obstacles with which the animal collided, as well as a small cost of visual acuity, I obtained the optimal visual acuity. I explored how this value depends on parameters such as visible distance, visible angle, turning ability, movement speed, and densities of food and obstacles in the field. If the animal's visual acuity is close to the optimal value and if the visual distance is greater for large eye size, the positive correlation between movement speed and eye size is greater when obstacles are more abundant, food items are rare, and the damage due to collision is large. In contrast, Leuckart's Law may not hold in environments with abundant food, rare obstacles, and small collision damage.

Model

Using computation simulations, I considered an animal moving in a field, avoiding obstacles and foraging for food items, and examined how its performance depends on visual ability. Figure 1 illustrates a simulated field, in which many obstacles and food items are randomly distributed. The field is modeled as a 10,000 × 10,000 square lattice with periodic boundary conditions. A fan-shaped object on the plane indicates the area visible to a moving animal located at the pivot of the fan. Large and small circles represent obstacles and food items, respectively. The location of the focal animal, or the pivot of the fan, is specified by two coordinates, (x, y). The animal also has a direction to move, which is given by the directional angle (θ). I assume that the animal moves at a constant speed v. These three variables specify the state of the animal.

The entire field contains a number of food items and obstacles that are not mobile and are distributed following Poisson point processes with constant densities. The animal is modeled as a point. When the animal encounters a food item, it consumes it; in contrast, when the animal hits an obstacle, it incurs damage. The number of obstacles is *r*, and the number of food items is *f*.

Movement and reorientation of the animal

The maneuvering ability of the animal is characterized by four parameters: visible distance *R* specifies how far the animal can see, and visible angle 2ω represents how wide an area the animal can see. The animal moves at a constant speed *v*. The spatial area the animal can see is in the shape of a fan (or a sector), the pivot of which is the animal's body. When the animal finds a food item or an obstacle, it may turn the direction of its locomotion to capture the food item or to avoid the obstacle. The maximum speed of change in the orientation per step is specified by the turning ability *s*. Thus, six parameters in total specify the simulation model: four parameters specify the animal's maneuvering ability, while two parameters describe the environment (densities of food items *f* and obstacles *r*).

The animal can see food items and obstacles that exist within the visible area (the fan-shaped area with radius *R* and angle 2ω, with the pivot directly on the animal's body). If there are no obstacles to avoid within the visible area and if there are one or more food items, then the animal attempts to reach them. The animal first examines the reachability to each food item as well as the distance to it, considering its turning ability. Among food items that are reachable, it attempts to reach the closest one. After consuming it, the same procedure repeats. In order to keep the number of food items constant, the food item consumed disappears and a food item appears at other point.

In contrast, if there are one or more obstacles within the visible area, the animal attempts to avoid collision, considering its turning ability. In calculating the path to avoid collision, the animal starts turning at the last moment that allows it to avoid collision. Avoiding collision with an obstacle has priority over food consumption. If there are multiple food items in the visible area, the animal first calculates the possible ways to reach each food item, considering its own turning ability as well as the possibility of collision with an obstacle on the way. If it is not possible to reach the food item without colliding with an obstacle, the animal excludes the food item from consideration. In other words, animals only approach food items that are accessible without collision.

Initial conditions

Before beginning the simulation, the 'radius for avoidance' is calculated to each obstacle. The radius for avoidance is defined as the radius of the circumference of a circle within which the moving animal can avoid certain obstacles if it engages in reorientation. This radius is determined when the radius of obstacles, movement speed, and turning ability are given.

The simulation was conducted using the following steps. A set of parameter values (R, v, s, ω), the spatial distributions of obstacles and food items, and the initial position of the moving animal were defined. The distributions of obstacles and food items were determined to avoid overlap with other obstacles and food items. The initial position of the moving animal was also set to avoid overlap with obstacles and food items.

The distribution of food items and obstacles and initial position of the animal were initially determined using random numbers. The animal then moved around in the simulated field for 10,000 steps. One movement step consists of reorientation, straight movement, and judgment of possible collision and possible food consumption. To remove the effect of the choice of initial conditions, the animal was allowed to move the first 100 movement steps without recording. I then began to record the number of collisions with obstacles and the number of food items consumed.

Number of encounters with food items and obstacles

Figure 2-a presents a contour plot of the results of simulations for the number of food items consumed. The horizontal axis is movement speed v, and the vertical axis is visible distance R. When the movement speed is slow, the animal cannot increase the number of food items consumed by adopting a longer visible distance (Fig. 2-a). In contrast, if the animal can move sufficiently quickly, it has a longer visible distance and consumes more food items than the animal with a shorter visible distance. Therefore, possessing a long visible distance is effective when the movement speed is sufficiently fast.

Figure 2-b illustrates a contour plot for the number of collisions with obstacles. If the movement speed is slow, the animal does not need a long visible distance, because it can avoid obstacles with a moderately long visible distance. In contrast, if the movement speed is fast, an animal with a short visible distance undergoes many collisions; hence, a swiftly moving animal requires a long visible distance.

Cost of vision and optimal visible distance

To explore the optimal visible distance for a given movement speed, I introduced the cost of vision. The cost of constructing and maintaining eyes is likely to be higher for elaborate eyes than for simple eyes, although there has been no clear experimental measurement of this cost. I assume that the fitness is:

$$\phi = \left(g - dh\right) \times \exp\left(-cR^2\right). \quad (1)$$

The number of food items consumed g and the number of collisions d can be calculated from computer simulations, as explained below. The constant h indicates the damage due to collision, relative to the benefit of food intake. I assume that the cost of eye size increases with visual ability in a quadratic manner. c is the coefficient of the cost of elaborating eyes.

I can obtain the optimal visible distance, R_{opt}, as the value that maximizes fitness φ for a given movement speed v. An optimal eye size exists and depends on the cost of eye size, as illustrated in Fig. 3.

Optimal visible distance increases with movement speed

I generated a number of simulation runs with different visible distances R and obtained the optimal visible distance R_{opt}. I then compared this value for different movement speeds v. Leuckart's Law postulates that R_{opt} and v should be positively correlated.

Figure 5 shows that the optimal visible distance is longer for faster-moving animals than for slower animals. This finding supports Leuckart's Law, i.e., movement speed and visual ability are positively correlated if I consider a positive correlation between eye size and visible distance (Land and Nilsson, 2012). Figure 4 shows that $\ln R_{opt}$ and $\ln v$ exhibit a linear relationship. I can consider the linear regression of the logarithmic value of optimal visible distance and the logarithmic value of movement speed $\ln v$: $\ln R_{opt} = \alpha \ln v + \beta$. From a number of simulation results with different v, I can estimate the speed sensitivity α as follows:

$$\alpha = Cov(\ln R_{opt}, \ln v) / Var(\ln v) \qquad (2)$$

which indicates the magnitude of dependence of R_{opt} on v. It is a quantity of no dimension, and is called 'elasticity.' In population biology, elasticity has been used to analyze proportional sensitivity (Kroon et al., 1986; Caswell, 2000).

I obtained the value of α, Eq. (2), which was always positive. Hence, Leuckart's Law holds in our model. However, the magnitude of speed sensitivity α varied with parameter sets, so I next examined the dependence of α on different parameters.

Figure 5 illustrates how speed sensitivity α depends on four parameters in the model, namely r, f, d, and c. I first set a standard set of parameter values and then examined how α changed when one of the parameters, e.g., k, increased after being multiplied by factors 1.3, 1.6, 1.9, 2.1, 2.4, and 2.7, while all other parameters remained at their standard values. Speed sensitivity α increased or decreased almost linearly with $\ln(k/k_0)$, where k_0 is the standard value of parameter k. The slope indicates the dependence of speed sensitivity α on the parameter k. I performed this procedure for each of the four parameters. In the example shown in Figure. 6, speed sensitivity α increased as r and d increased but decreased as f increased. Speed sensitivity α did not strongly depend on c.

This observed parameter dependence of α may depend on the choice of the standard set of parameters. To determine the variability of the slope for each parameter when the choice of the standard set of parameters changed, I performed a similar analysis for 16 different parameter sets, generated by considering high and low standard values for each parameter, the ranges of which differed by two-fold. I performed a sensitivity analysis for each of these 16 sets of parameters, as shown in Figure. 5. I then obtained the variability of the slope, namely the sensitivity of α to each parameter. Despite considerable variability in the slope, I never observed a change in the sign (see Figure. 6), which confirms that speed sensitivity α increased with the number of obstacles r and the collision damage d but decreased with the number of food items f. α was almost independent of the cost of eyes c.

Next, I performed a multi-variable analysis to assess how speed sensitivity α depends on the four parameters r, d, f, and c. It is important to note that interactions between different parameters are possible, which was excluded from the above analysis. I pooled all simulation α values for different combinations of the four parameters and performed a regression analysis on $\ln r$, $\ln d$, $\ln f$, $\ln c$, and their combinations, e.g., $(\ln r)(\ln d)$ or $(\ln r)(\ln f)$. This is a standard method for a generalized linear model (Kasuya, 2012). I then obtained the following regression formula, which excludes terms whose weights were not significant:

$$\alpha = 0.106 + 0.744 \ln r - 0.387 \ln f + 0.237 \ln d + 0.260 \ln r \ln d - 0.432 \ln r \ln f \quad (3)$$

The results again indicate that α depends on *r*, *f*, and *d*, but is independent of *c*. However, I also observed that the interaction terms between ln*d* and ln*r* and between ln*f* and ln*r* were statistically significant. Therefore, I present parameter dependence in contour plots in Figures. 7 and 8. Figure 7 is a contour plot of α. The horizontal axis is the logarithm of the number of obstacles, and the vertical axis is the logarithm of the damage of collisions. This figure suggests that a large *r* and a large *d* cause α to increase. Figure 8 includes two contour plots of α for *f* and *r*. The horizontal axes are for the logarithm of the number of obstacles, and the vertical axes are for the logarithm of the number of food items. From these results, I can conclude that large *f* (food abundance) and small *r* (obstacle density) cause α to decrease.

Discussion

Leuckart’s Law predicts that faster-moving animals tend to have larger eyes than slower-moving animals, because large eyes improve visual ability. Additionally, faster-moving animals need high visual acuity to avoid obstacles or to forage. Although this law seems plausible, the few empirical studies about this law have reached conflicting conclusions. In this study, I examined the conditions under which Leuckart’s Law holds, i.e., when a faster-moving animal would have larger eye size. I conducted computer simulations of an animal moving on a plane that contains many food items to consume as well as obstacles to avoid. After a sufficiently long simulation run, I obtained the number of food items consumed and the number of collisions with obstacles. The results confirmed that fast-moving animals need a long visible distance, whereas slow-moving animals need only a short visible distance. Because long visible distance is made possible by large eye size (Land and Nilsson, 2012), these results suggest that faster-moving animals are likely to have larger eyes, supporting Leuckart's Law. These findings suggest that obstacle avoidance and foraging for food items are the mechanisms behind Leuckart's Law. Walls (1942) stated that faster-moving animals have large eyes because of the necessity of collision avoidance, and other studies have concluded that avoiding collisions and navigating food resources over greater distances are the mechanisms behind this law (Brookes et al., 1999; Hall and Heesy, 2011; Heard-Booth and Kirk, 2012).

I obtained the optimal visual acuity by considering the number of food items consumed by a moving animal, the number of obstacles with which it collides, and a small cost of visual acuity. The optimal visible distance tended to increase with movement speed, forming a linear relationship when plotted on a logarithmic scale. I denoted the slope of the linear regression as α, i.e., 'speed sensitivity.' I then examined the parameter dependence of α and found that a larger number of obstacles r and more damage by collisions d tend to cause α to increase, whereas a larger number of food items f tends to cause α to decrease. In contrast, α did not depend on cost c of visual acuity.

Hall and Heesy (2011) directly measured eye size and flight speeds of birds and concluded that Leuckart's Law does not hold in birds, but Heard-Booth and Kirk (2012) concluded that the law does hold in mammals. Our theoretical results suggest that birds may navigate environments in which food availability is high and obstacles are relatively rare, whereas mammals may live in environments with low food availability, many obstacles, and high levels of damage from collisions. However, determining the identity and numbers of specific obstacles or food items and collision damage for each species would be difficult.

I cannot conclude that the different findings of the two previous direct measurements of Leuckart's Law can be entirely explained by variation in the abundances of obstacles and food items, damage from collisions, and the cost of visual acuity, as eye size is likely to be determined by selection pressures and constraints other than the four parameters I investigated. Activity pattern is another important factor determining eye size (Kay and Kirk, 2000; Garamszegi et al., 2002; Hall and Ross, 2006; Kirk, 2006; Werner and Seifan, 2006; Hall, 2008). Although almost none of the birds analyzed in Hall and Heesy (2011) were nocturnal, the dataset for mammals used by Heard-Booth and Kirk (2012) included several types of activity patterns: diurnal, cathemeral, and nocturnal, an aspect that was not addressed in our analysis. Future simulations should also consider chasing prey versus foraging, or include more complex avoidance behavior. However, to our knowledge, this paper is the first report that theoretically considers the conditions pertinent to Leuckart's Law, and I hope that our work will stimulate more theoretical research considering factors that were not addressed here, as well as empirical research focusing on other factors affecting eye size.

References

Brookes, M.d.L., Hanley, S., Laughling, S.B., 1999. The scaling of eye size and body mass in birds. Proc. Roy. Soc. Lond. Ser. B. 266, 405-412.

Burton, R.F., 2008. The scaling of eye size in adult birds: relationship to brain, head and body size. Vision Res. 48, 2345-2351

Caswell, H., 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81, 619-627

Eisthen, H.L., 1997. Evolution of vertebrate olfactory systems. Brain Behav. Evol. 50, 222-233

Kasuya, E., 2012. Study of data science by R 10, generalized linear model (Japanese), Kyoritsu Shuppan.

Fay, R.R., Popper, A.N., 2000. Evolution of hearing in vertebrates: the inner ears and processing. Hear. Res. 149, 1-10

Garamszegi, L.Z., Møller, A.P., Erritzøe J., 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc. R. Soc. Lond. Ser. B. 269, 961-967

Hall, M.I., Ross, C.F., 2007. Eye shape and activity pattern in birds. J. Zool. 271, 437-444

Hall, M.I, 2008. Comparative analysis of the size and shape of the lizard eye. Zoology 111, 62-75

Hall, M.I., Heesy, C.P., 2011. Eye size, flight speed and Leuckart's Law in birds. J. Zool. 283, 291-297.

Heard-Booth, A.N., Kirk, E.C., 2012. The influence of maximum running speed on eye size: a test of Leuckart's Law in mammals. The Anatomical Record, 295, 1053-1062.

Howland, H.C., Merola, S., Basarab, J.R., 2004. The allometry and scaling of the size of vertebrate eyes. Vision Res. 44, 2043-2065

Hughes, A., 1977. The topography of vision in mammals of contrasting life style: comparative optics and retinal organization. In The visual system in vertebrates, 613-756

Kay, R.F., Kirk, E.C., 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. Am. J. Phys. Anthropol. 113, 235-262

Kiltie, R.A., 2000. Scaling of visual acuity with body size in mammals and birds. Funct. Ecol. 14,226-234

Kirk, E.C., 2006. Effects of activity pattern on eye size and orbit aperture size in primates. J. Hum. Evol. 51, 159-170

de Kroon, H., Plaisier, A., van Groenendael, J., Caswell, H., 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67, 1427-1431

Land, M.F. Nilsson, D.E., 2012. Animal eyes: second edition. New York: Oxford University Press.

Leuckart, R.K.G.F., 1876. Organologie des Auges. Vergleichende Anatomie. In Handbuch der gesamten Augenheilkunde, 145–301. Graefe-Saemisch (Ed.). Leipzig: Engelmann.

Lisney, T.J., Collin, S.P., 2007. Relative eye size in elasmobranchs. Brain Behav. Evol. 69,266-279

Schultz, A.H., 1940. The size of the orbit and of the eye in primates. Am. J. Phys. Anthropol. 26, 389-408.

Walls., G.L., 1942. The vertebrate eye and its adaptive radiation. Bloomfield Hills, Cranbrook Institute of Science.

Werner, Y.L., Seifan, T., 2006., Eye size in geckos: asymmetry, allometry, sexual dimorphism, and behavioral correlates. J. morphol. 267,1486-1500

Figures

Figure 1

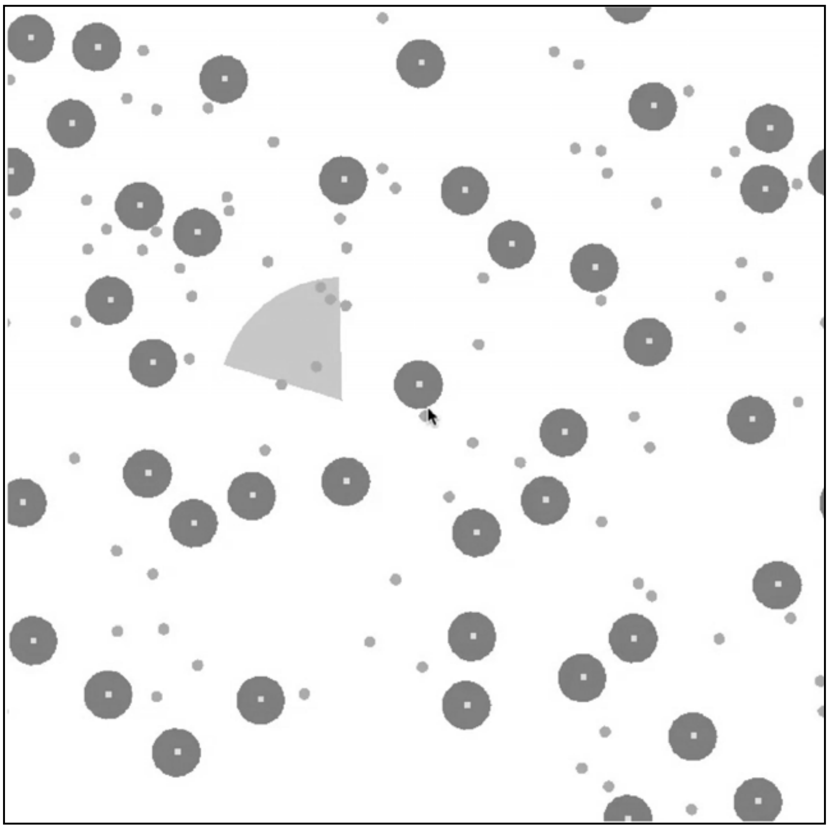


Figure 1. Scheme of the model. The area in which the animal moves is modeled as a 10,000 × 10,000 square lattice with periodic boundary conditions. The fan-shaped object represents the area visible to the moving animal. Large and small circles represent obstacles and food items, respectively.

Figure 2

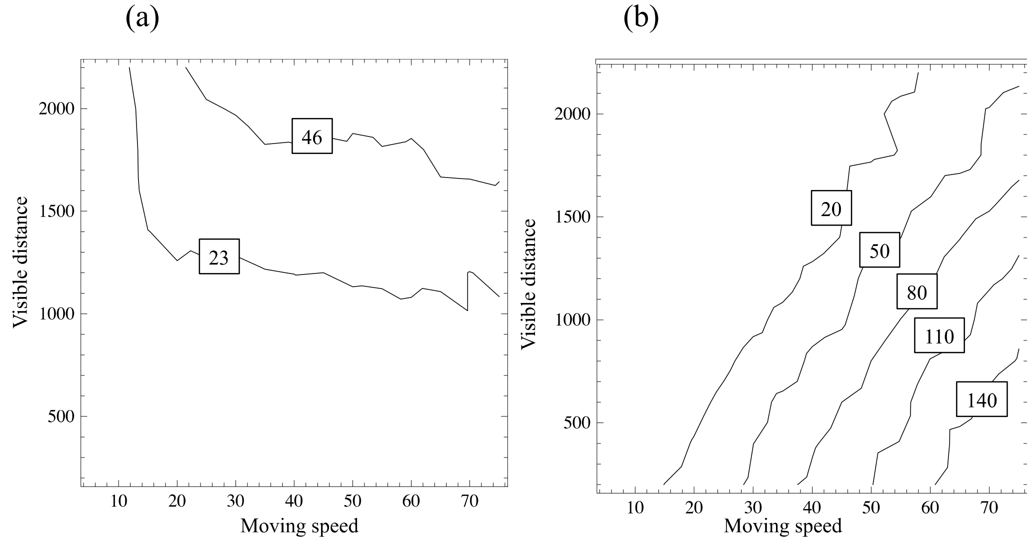


Figure 2. Results of simulations shown in contour plots. (a) Number of food items consumed. The horizontal axis is movement speed *v*, and the vertical axis is visible distance *R*. More food items are consumed with longer visual distances *R* and faster movement speeds *v*. (b) Number of collisions. Axes are the same as in (a). The risk of collision is higher for short visual distances *R* and faster movement speeds *v*. Parameters are: $r = 30, f = 40$.

Figure 3

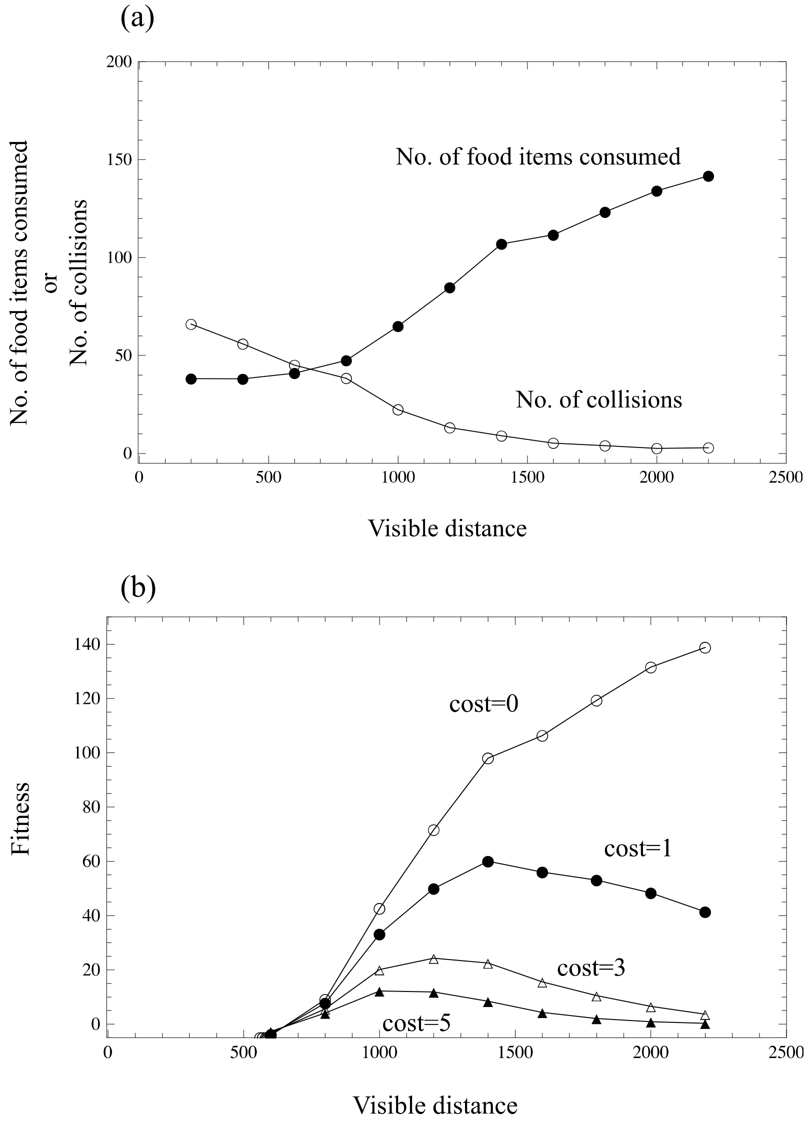


Figure 3. Optimal eye size. (a) Number of food items consumed and number of collisions versus visible distance. The horizontal axis is visible distance *R*. (b) Fitness calculated using Eq. (1). The horizontal axis is visible distance *R*, and the vertical axis is fitness calculated using Eq. (1). Parameters are: $r = 20, f = 40, v = 20$.

Figure 4

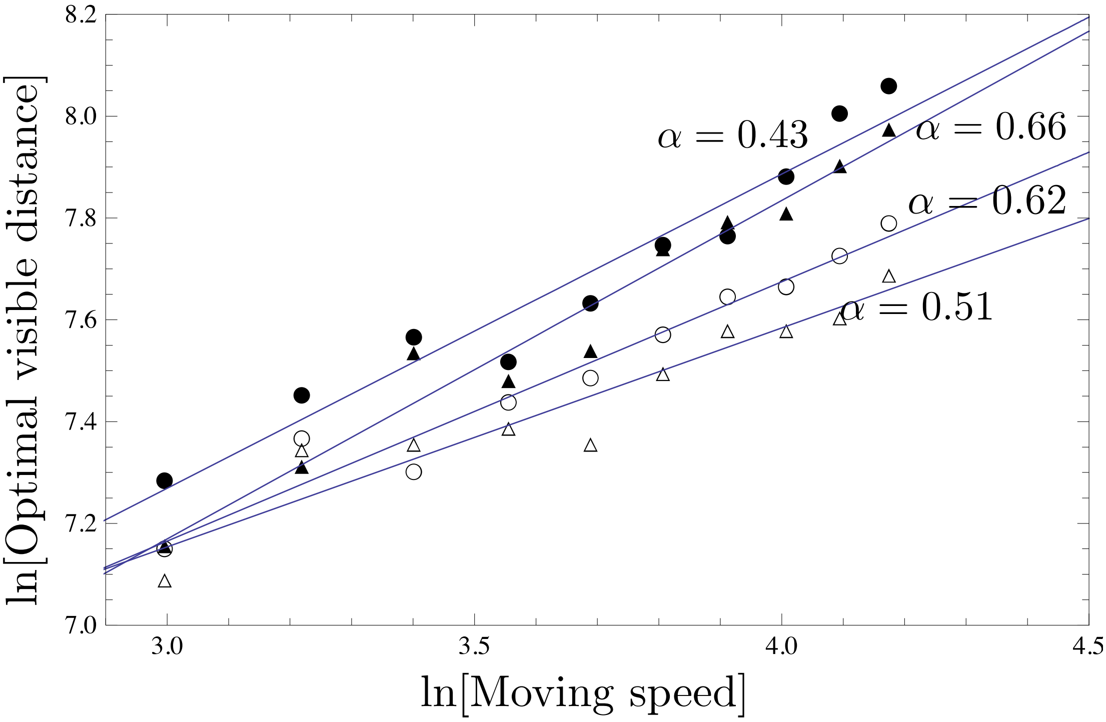


Figure 4. Optimal visible distance versus movement speed. The horizontal axis is the logarithm of movement speed ln$v$, and the vertical axis is the logarithm of optimal visible distance lnR_{opt}. Different symbols indicate different sets of values for the number of food items f and the number of obstacles r. Other parameters are: c = 3, d = 5. The slope of the regression line is denoted by α and is called the ‘speed sensitivity.’

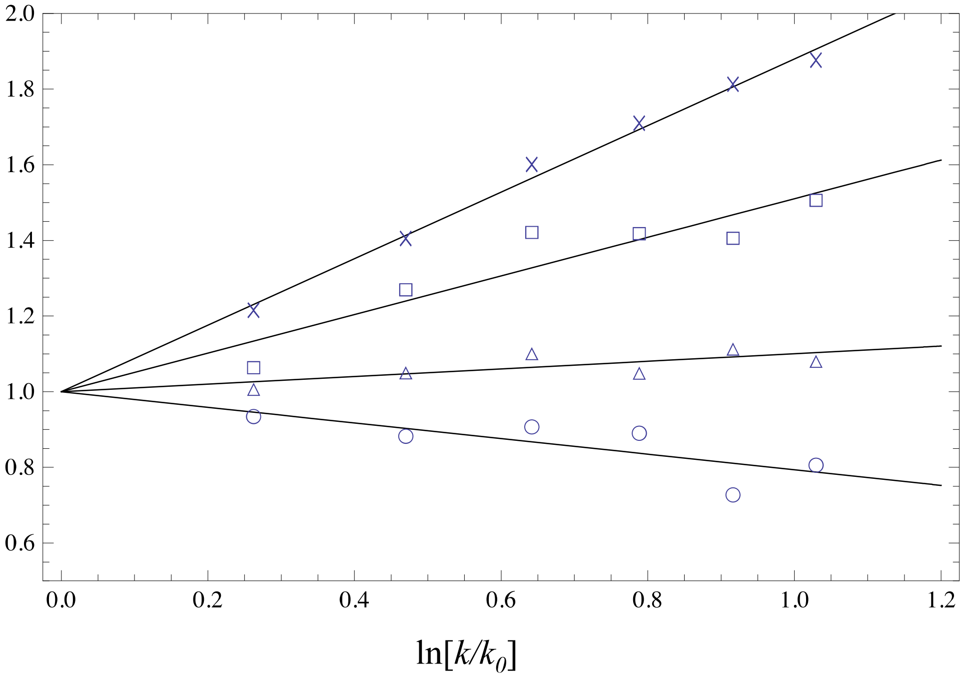


Figure 5. Speed sensitivity α depends on four parameters (*r*, *f*, *c*, and *d*). I chose the standard values of parameters as: $f = 40$, $r = 20$, $c = 3$, and $d = 3$. I increased the four parameters (e.g., *k*) by multiplying them by 1.3, 1.6, 1.9, 2.1, 2.4, and 2.7, with the other parameters unchanged. The horizontal axis is the change in the logarithm of *k* (i.e., $\ln[k / k_0]$), and the vertical axis is the change in α (i.e., α / α_0). Different symbols represent different parameters that were changed: crosses represent the number of obstacles *r*; circles represent the number of food items *f*; triangles represent the cost of eyes *c*; and squares represent the damage by collisions *d*.

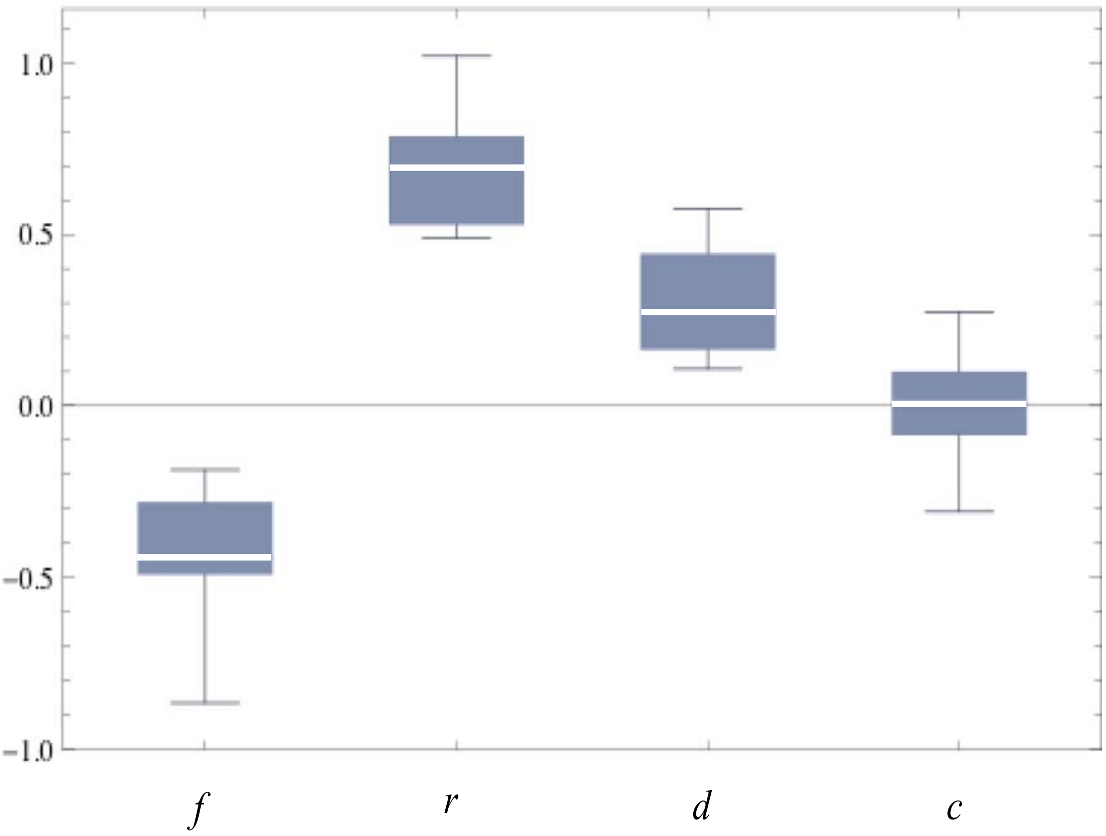


Figure 6. Sensitivity of α for each parameter. I performed the analysis shown in Figure. 5 for 16 different parameter sets, generated by combinations of high and low values of four parameters (ranges differed by two-fold). Parameters are: $f = 20$ and 40, $r = 10$ and 20, $c = 3$ and 6, $d = 3$ and 6.

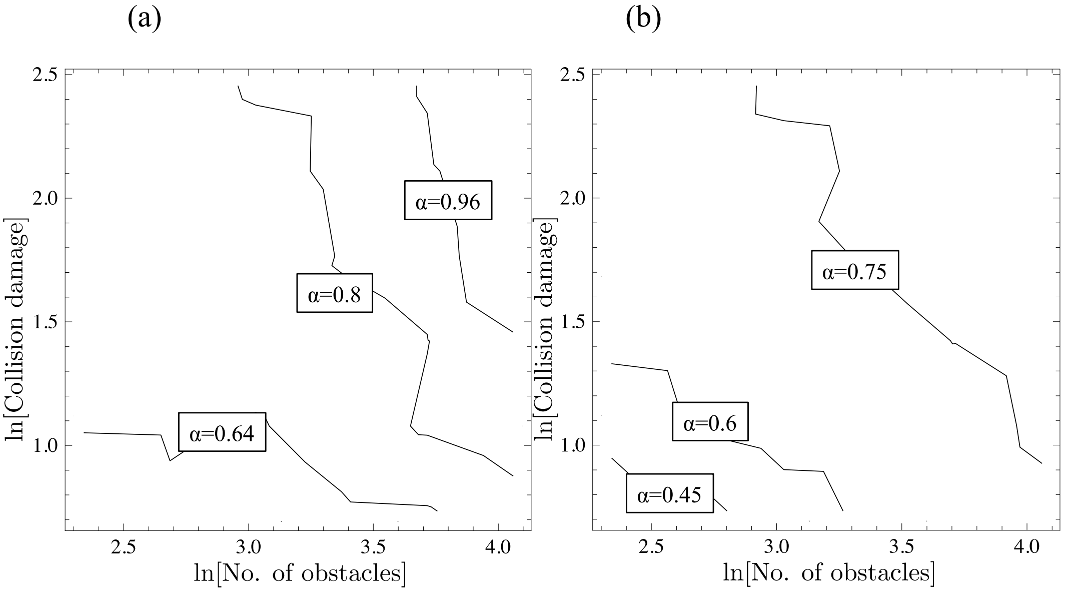
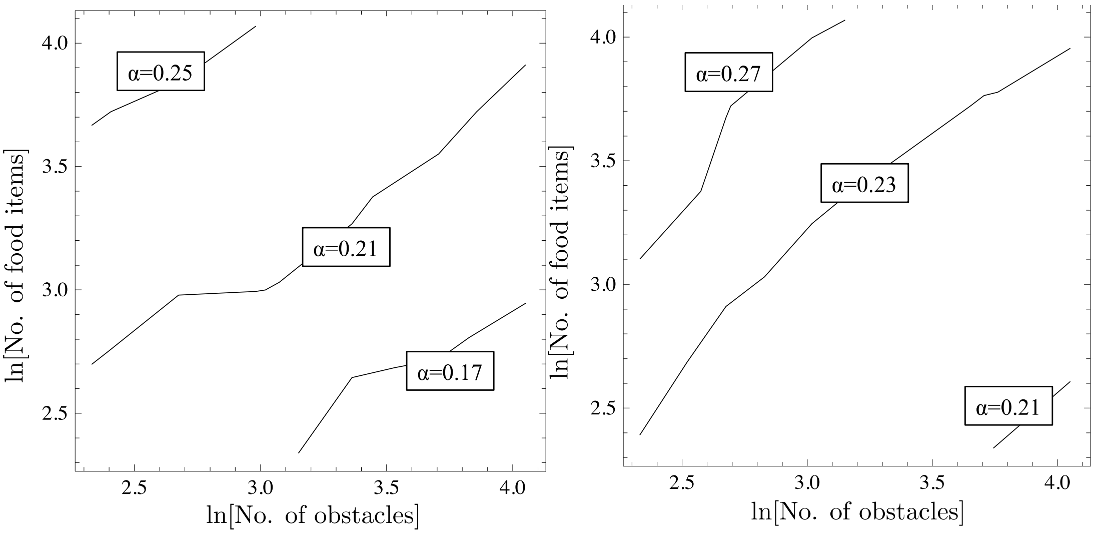


Figure 7. Contour plot of speed sensitivity α. The horizontal axis is the logarithm of the number of obstacles (ln*r*), and the vertical axis is the logarithm of the damage of collision (ln*d*). Dark color indicates a small α. Other parameters are: (a) $f = 30$, $c = 5$; and (b) $f = 60$, $c = 5$. Contours that are not parallel to each other indicate an interaction between the two parameters.

Figure 8



(a)

(b)

Figure 8. Contour plot of speed sensitivity α. The horizontal axis is the logarithm of the number of obstacles (ln$r$), and the vertical axis is the logarithm of the number of food items (ln$f$). Other parameters are: (a) $d = 2$, $c = 5$. (b) $d = 4$, $c = 5$.

Chapter 3

An integrated theoretical framework bridging evolution and learning behaviors in response to uncertain signals

The study of this chapter has done in collaboration with Dr. Tom Sherratt,

Introduction

All animals are constantly confronting the issue of which organisms to attack or not. This issue is associated with how animals respond to signals emitted by other individuals. For instance, insects that are not toxic have a similar coloration to the toxic species, termed Batesian mimicry. Consequently, many predators are faced with the choice of whether or not to eat the colorful insect (Nur 1970; Charlesworth and Charlesworth 1975; Turner 1987; Gavrilets and Hastings 1998; Holmgren and Enquist 1999; Speed 1999; Blows and Wimmer 2005). Animals confront the same problem when they sense the signals from potential predators or parasites. Cuckoo birds lay their eggs in the nests of other species (Brooke and Davies 1988; Rowland et al. 2007; Langmore et al. 2009; Stevens and Merilaita 2009; Stoddard and Stevens 2010; Stevens 2016). Regardless of the major fitness losses, host species sometimes attack their own eggs instead of parasite eggs as a wrong choice (Lotem et al. 1992; Moskát and Hauber 2007).

To understand the mechanism underlying decision making in response to signals, many mathematical frameworks have been proposed. Signal detection theory (Staddon and Gendron 1983; Wiley 1994; Wiley 2006) and multiarmed model (Bellman 1956; Bradt et al. 1956; Jones 1978) are commonly used frameworks and they are widely applied to biological phenomena. Each model describes the mechanism of decision making by different approaches. In signal detection theory, two signals are assumed: (1) “True signal,” which should be attacked, and (2) “False signal,” which should be not attacked. These two signals are slightly different, and the signals are sent to receivers with noise. This model is designed to determine the best threshold level of signals above which signal receivers decide to attack. If the threshold is very small, then almost all signals should be judged as “True,” and receivers will attack many “False” signals by mistake. Alternatively, if the threshold is very large, receivers refuse many “True” signals. The best threshold is determined by this tradeoff, and we consider this to be the basis of optimal decision making of animals.

Signal detection theory is frequently applied to many biological problems. Sherratt (2002) used this framework to describe the problem of imperfect mimicry in Batesian mimicry. Mimic organisms, which have slightly different phenotypes from the model species, are maintained. There are many hypotheses why imperfect mimicry is maintained (Edmunds 2000). Sherratt (2002) used signal detection theory to explore which hypothesis is supported. This article support "relaxed selection hypothesis," which means imperfect mimicry is maintained because selection pressure is suddenly relaxed when similarity reaches a certain level. Penney et al. (2012) tested this hypothesis experimentally, and obtained consistent results with the model. Rodriguez-Girones and Lotem (1999) applied the hypothesis to cuckoo birds. The authors changed the similarity between host and cuckoo eggs. They investigated which eggs are accepted if the host species decides to accept the eggs using the signal detection theory. Quite similar eggs are accepted, and dissimilar eggs are refused. Interestingly, host species only refuse their own eggs when the similarity between cuckoo eggs and host eggs is intermediate. This phenomenon is experimentally supported. Signal detection theory is widely applied to discuss the evolutionary threshold in decision making.

There are also many models that describe decision making with learning. These models basically describe the situation when animals receive some information and gradually change their behavior based on experience. Determining whether animals gather more information or change their behavior by using the received information is called "exploration-exploitation trade-off" (Cohen et al. 2007), and the basis of this trade-off is described in the "multiarmed bandit" model (Bellman 1956; Bradt et al. 1956; Jones 1978). Hypothetical agents manipulate a slot machine that have two arms. The average rewards from the two arms are different. Optimal agents first manipulate both arms and try to estimate the average reward form each arm. Finally, they only pull the best arm decided by their experience. This model had been widely applied to the choice of foraging sites (Green 1980; Ollason 1980; Iwasa et al. 1981; McNamara and Houston 1985).

The "Multiple bandit" is also used in models describing decision making to signals. Sherratt (2011) applied this model to the problem of a predator choosing prey items that emit unknown signals. The author showed if the frequency of encountering the signal is high, animals sample the signal many times and gain information. However, if the signal is rare, animals reject the signal after a few sampling events. Furthermore, if animals have a low chance of predation, they become pessimistic. Thus, it was argued that neophobia is observed if animals behave using the multiple bandit model.

Each model represents biological phenomena in a certain situation. However, animals usually decide their behavior using both instinct and plasticity. The problem which behavior is based on instinct (innate) and which is on plasticity (acquired) is considered as innate acquired problem (Bateson and Mameli 2007). Many studies discuss whether a behavior is innate or acquired in many organisms. Kawamura et al. (2017) showed that the juvenile African cat fish *Clarias griepinus* prefers red and blue colored food items, and concluded that this behavior is an innate trait. In another study, Bhadra and Bhadra (2014) found that adult dogs prefer meat, but pups have no preference from meat, and argued that the preference for meat by adults is an acquired trait, not innate. However, it remains difficult to distinguish when animals behave innately and when they behave based on learning. This problem cannot be solved by existing models.

Here, we construct a new model to describe innate acquired problems. We extend the learning model of Sherratt (2011) by considering evolutionary processes. In particular, we represent innate behavior as the change of parameters of the initial prior distribution in the learning model. Using this model, we apply one example of an existing biological problem, which is aversion by innate or learning. We show that when the cost of attack to the signals (toxicity, predation rate, or something) is high, and when the frequency of unfavorable signals is high, animals avoid the signals by innate behavior. In contrast, animals avoid signals by learning under the opposite conditions.

Model and results

The learning model is basically the same as that developed by Sherratt (2011). Here, we describe the model conditions briefly (see Sherratt (2011) for more details). The model describes the scenario in which a predator encounters a relatively novel prey that emits some signals and the predator decides to eat the prey or not. This prey is chemically defended with probability p, and is palatable with probability 1-p. Both unpalatable and palatable prey emit the same signals for predators and predators cannot distinguish the prey should be attacked from prey should be avoided. If the predator attacks the prey, the predator incurs a cost c with probability p, or gains benefit b with probability 1-P. It is clear that the predator should attack the prey if $p < b/(b+c)$, because this equation means the probability of encountering chemically defended prey is less than the mean benefit gained from attack. In contrast, the predator should not attack if $p > b/(b+c)$. However, predators do not know the true value of p; thus, they do not know how frequently prey individuals are chemically defended. Predators can gain information about the frequency of encountering chemically defended prey, and update their estimated p value. Finally, predators decide to eat prey based on this experience.

It is assumed that the predator encounters prey individuals that are chemically defended r times in a total of n prey items sampled ($r < n$). Thus, the probability that the event occurs is described by binominal probability as:

$$\Pr(X = r) = \binom{n}{r} p^r (1-p)^{n-r}$$

If we assume the prior distribution of the learning process as beta distribution, posterior distribution is also explained by beta distribution. In particular, when prior distribution is Beta(α_p, β_p), posterior distribution can be explained as Beta(α_p+r, β_p+n+r).

We use the payoff to decide whether the predator should attack or not. There is a total of N prey items in the environment that the predator could potentially sample in its lifetime. The predator encounters prey individuals n times and eats chemically defended prey items r times. With any predator experience state (r, n), the maximum payoff from the remaining (N-n) trials is represented by S(r, n). If the predator does not attack at all in future (N-n) trials, the future reward of $S_D(r,n) = 0$. Alternatively, if the predator attacks prey individuals, it risks eating chemically defended prey, but it also gains information and enhances the accuracy of estimating P, which is the exploration-exploitation trade-off. This payoff is denoted as $S_A(r,n)$, and we explain S(r,n) as;

$$S(r,n) = \max[S_D(r,n), S_A(r,n)]$$

where

$$S_D(r,n) = 0$$

and

$$S_A(r,n) = \pi_p(r,n)[S(r+1,n+1) - c] + \left(1 - \pi_p(r,n)\right)[S(r,n+1) + b]$$

π_p is the estimated value of P (frequency of unpalatable prey) in its experience state (r, n). We used the mean value of beta distribution: $\pi_p = (\alpha+r)/(\alpha+\beta+n)$. The value of π_p changes when the predator encounters prey individuals. The predator stops attacking at $S_d > S_a$ when it encounters many unpalatable prey individuals and π_p becomes larger.

Many analyses are conducted in Sherrat (2011) using this model. All of the results in Sherratt (2011) use the parameters $\alpha = 1, \beta = 1$; thus, the parameters in the initial prior distributions are fixed. However, the results of this model completely change depending on the parameters in prior distributions.

Figure 1 presents the score value of each (α, β) parameter set. Predators are pessimistic if α is larger than β, and optimistic if β is larger than α. Predators eat prey items in accordance with the optimal sampling rule, and they encounter 500 prey items ($N = 500$). The score value is equal to b × (the number of palatable prey items eaten) – c × (the number of unpalatable prey items eaten). Thus, the maximum and minimum score values are 500 and -500, respectively. Figure 1-a is a contour plot where $p = 1.0$, which means that all prey items are chemically defended. Predators perform the maximum score (= 0) with large α and small β. Pessimistic predators are favored because all prey items are unpalatable. Figure 1-*b* is a contour plot with $p = 0$, which means that all prey items are undefended. Predators perform the maximum score (= 500) with large β and small α. Predators receive large benefits if predators eat prey items positively.

Figure 2-a and 2-b presents the cost dependence of the score when all prey items are chemically defended ($p = 1$). c is 0.2 in figure 2-a, and 3 in figure 2-b. When the cost declines, the area where predators perform the maximum score becomes narrower. Predators eat prey items more positively because the risk of predating unpalatable prey is low. In contrast, when the cost rises, the area where predators perform the maximum score widens, because predating risk is high. Figure 2-c and 2-d demonstrates the cost dependence of the score when all prey items are chemically undefended ($p = 0$). c is 0.2 in figure 2-c, and 3 in figure 3-d. This result shows the same tendency to the case of $p = 1$.

Figures 1 and 2 are under the condition that $p = 1$ and 0. Figure 3 presents $0 < p < 1$. Under this condition, the score differs with predator experience, thus we conducted stochastic simulation. Each value is the mean value of 1,000 iterations. Here, predators encounter 500 prey items ($N = 500$), and the benefit and cost from predation is 1 ($b = c = 1$). Figure 3-a is a contour plot with $p = 0.5$. The score values are about 0 in each parameter set (α, β). Pessimistic predators do not eat prey items and the score becomes 0. Optimistic predators eat prey items, of which almost half are palatable and almost half are unpalatable, so the score becomes 0. Figure 3-b is a contour plot with $p = 0.8$, whereby 80% of prey items are unpalatable. Under this condition, pessimistic predators (large α and small β) obtain high scores because more than half of prey items are unpalatable. If p is less than 0.5, the tendency becomes to be reversed.

Figure 4 presents the cost dependence of the score ($p = 0.8$). c is 0.2 in figure 4-a, and 3 in figure 4-b. When c increases, the score decreases. There are two reasons for this change: (1) they do not eat prey items positively (shown in result 2); (2) the negative effect of the score increases when they eat unpalatable prey. If c increases, pessimistic predators become favorable. This threshold should be defined as the balance among cost, benefit, and the frequency of defended prey. When c decreases, the score increases larger and the parameter area where they do not attack prey items becomes narrower. This phenomenon occurs because predators know that the risk of eating unpalatable prey is small and they can be more optimistic predators.

These results are generated by changing the parameters of the initial prior distribution values. These values are fixed in Sherratt (2011) because animals without learning are considered to have no information about the environment. Changing the parameters in the initial prior distributions is corresponding to that animals have information about the environment without learning. In other words, the values in prior distributions parameters are innate (evolutionary) traits. We constructed the joint model of leaning (acquired) and evolution (innate) by assuming that the parameters in the initial prior distribution are evolutionary parameters.

Evolutionary Analysis

Overview

We assumed the parameters in the initial prior distributions (α, β) were evolutionary parameters, and we calculated the distributions of these parameters at evolutionary end points. An individual has an initial parameter set (α, β). It starts the learning process from its initial parameter set (α, β). We calculated the score based on the number of palatable and unpalatable prey items it ate after experiencing N trials, as well as the process described in the learning model section. Animals with high scores produce many offspring with similar initial traits to the parent. We ran this procedure repeatedly and stopped the calculation when the distribution of the frequency of the initial prior distribution no longer changed.

Model and results

We assumed that $M = I \times J$ type parameter sets were generated by the combination of α and β. I is corresponding to the number of patterns of α values and J is corresponding to the number of patterns of β values and and we defined the fitness of each initial parameter set as follows:

$$W_{ij} = \frac{W_0 + A_{ij}}{\frac{1}{M}\sum_j^J \sum_i^I (W_{ij} + A_{ij})}$$

where W_0 is the baseline fitness, and A_{ij} is the score after N trials in the learning process. A_{ij} was calculated as; $A_{ij} = b \times$[number of palatable prey that were attacked]-$c \times$[number of unpalatable prey that were attacked], using the same score as in the previous results. By using this fitness value, we conducted the evolutionary simulation. We assume that the individual reproduce offspring by proportional to their fitness. We also assume the mutation as the individual with parameter (α, β) reproduce the offspring with slightly different parameter set (i.e. combination of $\alpha \pm \Delta\alpha$ or α and $\beta \pm \Delta\beta$ or β) with probability μ. We did not assume any competition between predators or natural death, and all types increased over time. The results are shown with the frequency of each trait, and we stopped the calculation when the frequency of each type no longer changed.

Figure 5 presents the fraction of each strategy at the evolutionary endpoint. Here, $p = 0.8$, whereby 80% of prey items are unpalatable. The light color means high frequency, and the dark color means low frequency. Based on this result, pessimistic prior evolves. It is an intuitive result, because most prey items are unpalatable, so pessimistic predators are favored. The trait with the parameter that has a similar value to the best parameter also has high frequency. This result is obtained because the fitness is not so different from the fitness of individuals, with the best parameter being due to their traits being immediately adjusted in learning process.

By using the model that we constructed, we are able to explore an example of innate acquired problems. Figure 6 shows that the condition that predators should avoid prey items innately or by learning. Here, we conducted the evolutionary calculation and classified it as avoiding innately if pessimistic predators evolve (large α and small β), because predators with large α and small β do not eat prey items completely. The horizontal axis in Figure 6 is the cost of predation, c, and vertical axis is the frequency of unpalatable prey, p. The light area is where a predator which avoid signals innately evolves. The dark area is where a predator which avoids signals by learning evolves. Based on this result, animals use innate avoidance when the cost of attacking unprofitable signals is high, and they avoid by it leaning when the cost is low. Furthermore, animals avoid signals innately when they encounter signals frequently, and the animals avoid signals by learning when the signals are relatively rare.

Discussion

When animals receive some signal from the environment, they decide what action to take (attack, avoidance, staying, and so on). This decision-making process is decided by both, or either, innate and acquired traits. Animals seem to behave appropriately depending on the situation. There are extensive discussions about innate acquired problems, but the rules driving these two types of decision-making processes (innate/acquired) remain poorly understood. Here, we constructed an extended learning model with evolution to determine the situation when animals behave innately or by leaning. We assumed that the parameters in initial prior distribution are innate traits, and we conducted our evolutionary analysis by assuming that the parameters in the prior distribution were evolutionary traits.

Dependence on parameters in the initial prior distribution

We found that the results of the learning process noticeably change when the parameters in the initial prior distribution changes. In particular, pessimistic predators immediately stop attacking when they attack unprofitable prey a few times, whereas optimistic predators continue attacking until they eat unpalatable prey many times. Shettleworth (1972) reported how experience influences preferences in birds. The birds had already learned that blue water is palatable. After that, the birds were presented with blue water that had an unprofitable taste or clear water with the same taste as the blue water. The authors showed that birds needed more time to avoid blue water that was pre-perceived as good tasting than to avoid clear water that they had never experienced. This result supports our model findings, whereby the time that animals spend learning and deciding varies depending on the prior distribution.

Evolutionary Analysis

There are many reports about instinctive behavior, whereby animals have some information about signals without learning and experience (Marler 1990; Schiestl 2017). For instance, Chamaille-Jammes et al. (2014) reported avoidance behavior in deer. The authors showed that black-tailed deer (*Odocoilus hemionus sitkensis*) avoid models of wolves (*Canis lupus*), which became extinct over 100 years ago, more strongly than models of black bears (*Ursus americanus*), which still coexist with deer. Deer could not learn the wolf signals because the wolf no longer exists. Therefore, the authors concluded that deer strongly avoid wolves by innate preference. Our model assumed that animals have some way of evaluating signals (e.g., palatable or unpalatable) without learning, and that this assumption supports innate behavior in nature.

Our model simply predicted that profitable traits in the environment evolve. The trait with the parameter set that had the highest score, and that had parameters of similar value to the best parameter, increase. Individuals with parameters that had similar values to the best parameter might increase because fitness is similar to that of individuals with the best parameter, due to their adjusting their traits immediately through the learning process. Thus, fitness is decided through a process in which some initial prior distributions are adjusted to better traits depending on the environment. Darmaillacq et al. (2004) reported the adjustment of innate preference by experience. Cuttlefish (*Sepia officinalis*) choose shrimp (*Crangon crangon*) as food when the choice test is done soon after hatching; thus, cuttlefish prefer shrimp as prey items, innately. However, cuttlefish start to prefer other prey items more than shrimp when given other prey items, repeatedly, as juveniles; thus, they adjust their food preference through experience, despite having the initial trait (prior distribution without learning) of preferring shrimp. Thus, our model description, in which initial prior distribution is adjusted through leaning, strongly reflects actual situations in nature.

Avoidance by innate or acquired behavior

The model predicts that animals use innate avoidance when the cost of attacking unprofitable signals is high, and they avoid these signals by learning when the cost is low. In fact, animals avoid some signals where cost seems high, innately. Sea turtles avoid shark models (visual signal) innately (Bostwick et al. 2014). The Barton Springs Salamander, *Eurycea sosorum,* avoids the smell (chemical signal) of Largemouth Bass, *Micropterus salmoides*, innately (Desantis et al. 2013). Domestic chicks avoid the agitated buzzing (auditory signal) of *Bombus terrestris*, innately (Rowe and Guilford 1999). All of these signals these induce major damage or death if animals do not avoid them.

Botham et al. (2006) explored the response of guppies (*Poecilia reticulata*) to signals with different costs (three predators the pike cichlid, *Crenicichla frenata*; the blue acaracichlid, *Aequidens pulcher*; and the wolf fish, *Hoplias malabaricus*) under laboratory conditions. The pike cichlid is the greatest predator of guppies, eating them frequently in nature. The other two species eat guppies if given as food, but do not eat guppies much in nature. The guppies responds more strongly to pike cichlids than to other predators because they had a higher cost to guppies, supporting our model prediction.

Our model predicts that animals avoid signals innately when they encounter signals frequently; thus, animals avoid by learning when signals are relatively rare. This prediction is supported by the experimental results of Stapley (2003) on the lizard, *Pseudomoia entrecastauxii*, and three predators (white-lipped snake, *Drysdalia coronoides*; red-bellied black snake, *Pseudechis porphyriacus*; and small-eyed snake, *Rhinoplocephalus nigrescens).* The density of white-lipped snakes is relatively higher than the other two species in the area where the lizard is found. Stapley (2003) found that laboratory-reared lizards (i.e., no prior experience of snakes) avoided the smell of white-lipped snake (high density) more than the smell of the other two snake species (low density). The largest difference among these three predators is frequency of the lizard encountering them. Thus, this experimental result supports our model prediction that animals avoid signals innately when it is encountered frequently.

Model extension and future works

This study presented a simple model of learning and evolution for decision based on signals. This model could be extended and analyzed in various ways. For instance, if the effect of competition or the way of learning is explained based on how certain animals are introduced, the model could be used to discuss the actual behavior of real animals. The variation of prey or environmental change can be considered as simple extension. Animals exhibit plasticity (e.g. learning) to cope with uncertainty and environmental change (Dukas 1998). Rhoades et al. (2018) demonstrated that the innate preference of cats significantly differs both within and among species. Variance in innate preferences may differ among species due to differences in their life cycles or environmental changes. If we could explain a given environmental change or key components of the life cycles of each species with our model, we could explore what drives differences in innate preferences.

Innate acquired problems have been discussed for many animals, but many problems still remain. However, knowledge remains limited about when animals adopt innate behavior versus acquired behavior. Our study suggested a model to resolve this problem, with mathematical models possibly representing a first step towards understanding innate acquired problems. The framework we constructed in this paper is quite simple and could be expanded in many ways. In conclusion, we anticipate that the model developed here could enhance future studies seeking to understand how animals use innate acquired behavior.

References

Bateson, P., & Mameli, M. (2007). The innate and the acquired: useful clusters or a residual distinction from folk biology? *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *49*(8), 818-831.

Bellman, R. (1956). Dynamic programming and Lagrange multipliers. *Proceedings of the National Academy of Sciences*, *42*(10), 767-769.

Bhadra, A., & Bhadra, A. (2014). Preference for meat is not innate in dogs. *Journal of Ethology*, *32*(1), 15-22.

Blows, T. R., & Wimmer, B. J. (2005). A simple mathematical model for Batesian mimicry. *Discrete Dynamics in Nature and Society*, *2005*(1), 87-92.

Bostwick, A., Higgins, B. M., Landry Jr, A. M., & McCracken, M. L. (2014). Novel use of a shark model to elicit innate behavioral responses in sea turtles: Application to bycatch reduction in commercial fisheries. *Chelonian Conservation and Biology*, *13*(2), 237-246.

Botham, M., Kerfoot, C., Louca, V., & Krause, J. (2006). The effects of different predator species on antipredator behavior in the Trinidadian guppy, *Poecilia reticulata*. *Naturwissenschaften*, *93*(9), 431.

Bradt, R. N., Johnson, S., & Karlin, S. (1956). On sequential designs for maximizing the sum of n observations. *The Annals of Mathematical Statistics*, *27*(4), 1060-1074.

Brooke, M. d. L., & Davies, N. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, *335*(6191), 630.

Chamaillé-Jammes, S., Malcuit, H., Le Saout, S., & Martin, J.-L. (2014). Innate threat-sensitive foraging: black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. *Oecologia*, *174*(4), 1151-1158.

Charlesworth, D., & Charlesworth, B. (1975). Theoretical genetics of Batesian mimicry II. Evolution of supergenes. *Journal of Theoretical Biology*, *55*(2), 305-324.

Cohen, J. D., McClure, S. M., & Angela, J. Y. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *362*(1481), 933-942.

Darmaillacq, A.-S., Dickel, L., Chichery, M.-P., Agin, V., & Chichery, R. (2004). Rapid taste aversion learning in adult cuttlefish, *Sepia officinalis*. *Animal Behaviour*, *68*(6), 1291-1298.

DeSantis, D. L., Davis, D. R., & Gabor, C. R. (2013). Chemically mediated predator avoidance in the Barton Springs salamander (*Eurycea sosorum*). *Herpetologica*, *69*(3), 291-297.

Dukas, R. (1998). *Cognitive ecology: the evolutionary ecology of information processing and decision making*: University of Chicago Press.

Edmunds, M. (2000). Why are there good and poor mimics? *Biological Journal of the Linnean Society*, *70*(3), 459-466.

Gavrilets, S., & Hastings, A. (1998). Coevolutionary chase in two-species systems with applications to mimicry. *Journal of Theoretical Biology*, *191*(4), 415-427.

Green, R. F. (1980). Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theoretical Population Biology*, *18*(2), 244-256.

Holmgren, N. M., & Enquist, M. (1999). Dynamics of mimicry evolution. *Biological Journal of the Linnean Society*, *66*(2), 145-158.

Iwasa, Y., Higashi, M., & Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. *The American Naturalist*, *117*(5), 710-723.

Jones, P. (1978). On the two armed bandit with one probability known. *Metrika*, *25*(1), 235-239.

Kawamura, G., Bagarinao, T. U., Asmad, M. F. B., & Lim, L.-S. (2017). Food colour preference of hatchery-reared juveniles of African catfish *Clarias gariepinus*. *Applied Animal Behaviour Science*, *196*, 119-122.

Langmore, N., Stevens, M., Maurer, G., & Kilner, R. (2009). Are dark cuckoo eggs cryptic in host nests? *Animal Behaviour*, *78*(2), 461-468.

Lotem, A., Nakamura, H., & Zahavi, A. (1992). Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behavioral Ecology*, *3*(2), 128-132.

Marler, P. (1990). Innate learning preferences: signals for communication. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *23*(7), 557-568.

McNamara, J. M., & Houston, A. I. (1985). Optimal foraging and learning. *Journal of Theoretical Biology*, *117*(2), 231-249.

Moskát, C., & Hauber, M. E. (2007). Conflict between egg recognition and egg rejection decisions in common cuckoo (*Cuculus canorus*) hosts. *Animal Cognition*, *10*(4), 377-386.

Nur, U. (1970). Evolutionary rates of models and mimics in Batesian mimicry. *The American Naturalist*, *104*(939), 477-486.

Ollason, J. (1980). Learning to forage optimally? *Theoretical Population Biology*, *18*(1), 44-56.

Penney, H. D., Hassall, C., Skevington, J. H., Abbott, K. R., & Sherratt, T. N. (2012). A comparative analysis of the evolution of imperfect mimicry. *Nature*, *483*(7390), 461-464.

Rodriguez-Girones, M. A., & Lotem, A. (1999). How to detect a cuckoo egg: a signal-detection theory model for recognition and learning. *The American Naturalist*, *153*(6), 633-648.

Rowe, C., & Guilford, T. (1999). Novelty effects in a multimodal warning signal. *Animal Behaviour*, *57*(2), 341-346.

Rowland, H. M., Speed, M. P., Ruxton, G. D., Edmunds, M., Stevens, M., & Harvey, I. F. (2007). Countershading enhances cryptic protection: an experiment with wild birds and artificial prey. *Animal Behaviour*, *74*(5), 1249-1258.

Schiestl, F. P. (2017). Innate receiver bias: Its role in the ecology and evolution of plant–animal interactions. *Annual Review of Ecology*, *Evolution*, *and Systematics*, *48*, 585-603.

Sherratt, T. N. (2002). The evolution of imperfect mimicry. *Behavioral Ecology*, *13*(6), 821-826.

Sherratt, T. N. (2011). The optimal sampling strategy for unfamiliar prey. *Evolution: International Journal of Organic Evolution*, *65*(7), 2014-2025.

Shettleworth, S. J. (1972). The role of novelty in learned avoidance of unpalatable ‘prey’ by domestic chicks (*Gallus gallus*). *Animal Behaviour*, *20*(1), 29-35.

Speed, M. (1999). Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evolutionary Ecology*, *13*(7-8), 755-776.

Staddon, J., & Gendron, R. P. (1983). Optimal detection of cryptic prey may lead to predator switching. *The American Naturalist*, *122*(6), 843-848.

Stapley, J. (2003). Differential avoidance of snake odours by a lizard: evidence for prioritized avoidance based on risk. *Ethology*, *109*(10), 785-796.

Stevens, M. (2016). Color change, phenotypic plasticity, and camouflage. *Frontiers in Ecology and Evolution*, *4*, 51.

Stevens, M., & Merilaita, S. (2009). Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1516), 423-427.

Stoddard, M. C., & Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20092018.

Turner, J. R. (1987). The evolutionary dynamics of Batesian and Muellerian mimicry: similarities and differences. *Ecological Entomology*, *12*(1), 81-95.

Wiley, R. H. (1994). Errors, exaggeration, and deception in animal communication. *Behavioral Mechanisms in Evolutionary Ecology*, 161, 157-189.

Figure 1

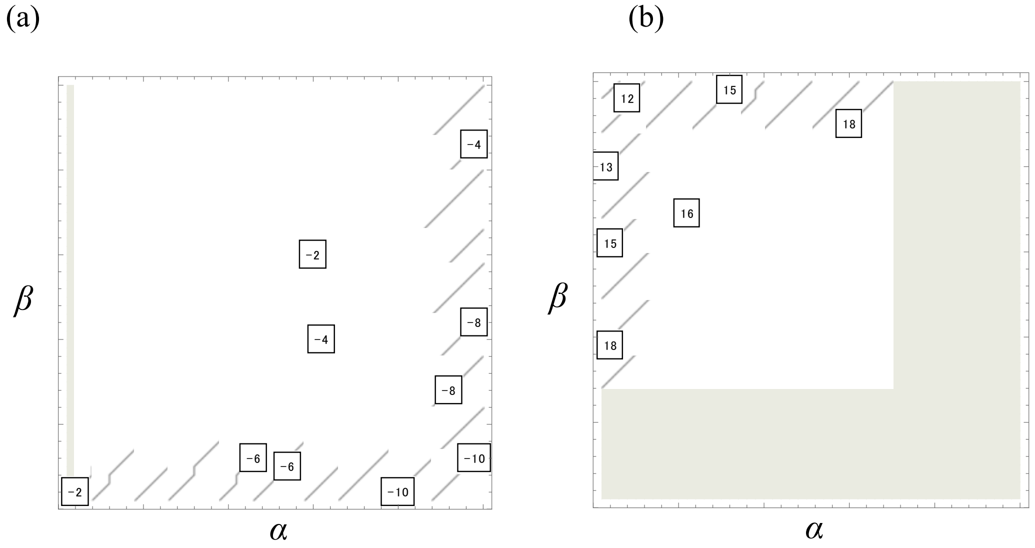


Figure 1. Score plot of each parameter set for the initial prior distribution. Horizontal axis represents α and vertical axis represents β; the frequency of unpalatable prey, p, is (a) 1.0 and (b) 0. Parameters are; $b = 1$, $c = 1$, $N = 500$.

Figure2

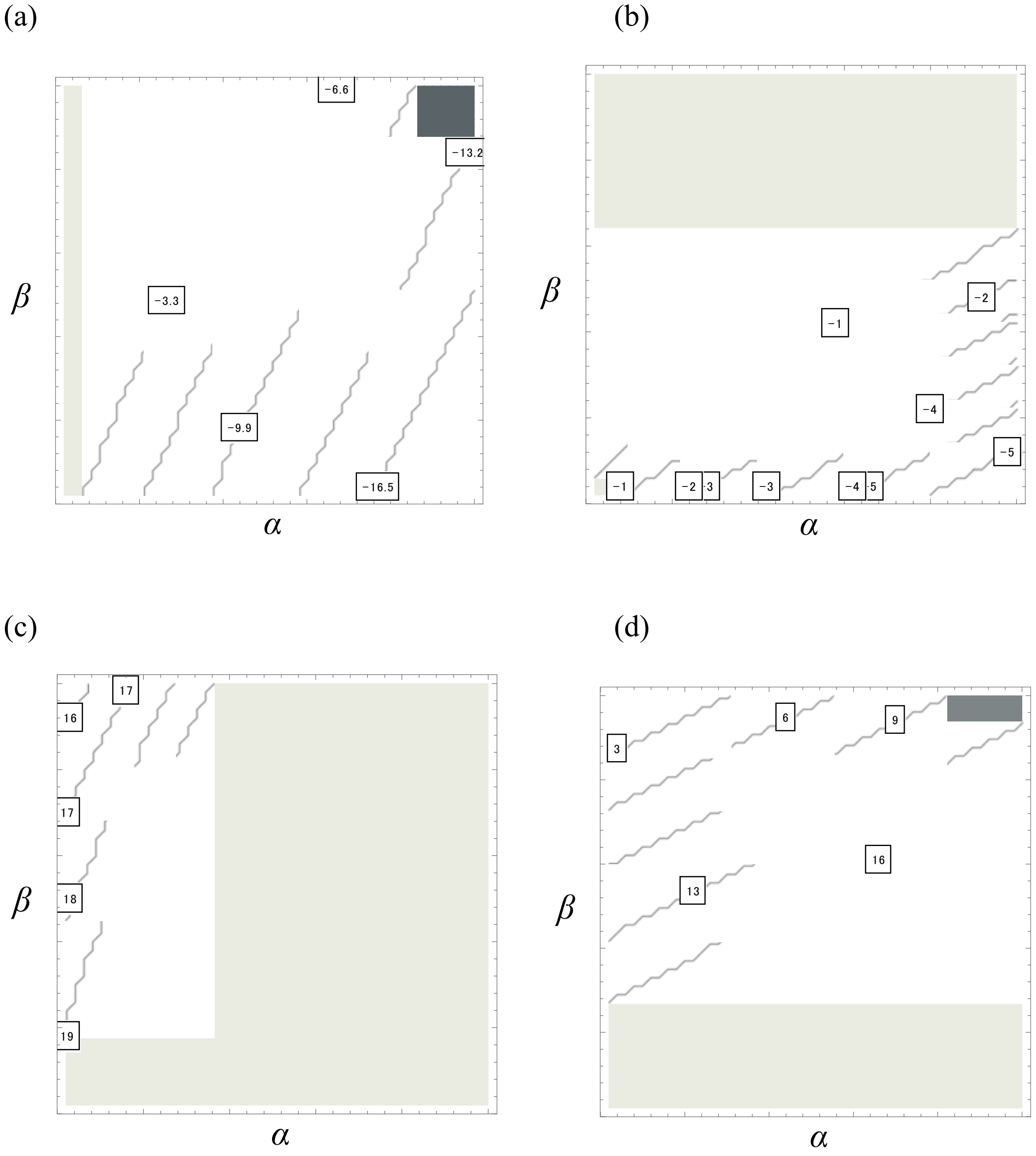


Figure 2. Cost dependence of the score plot. (a) p = 1 and c = 0.2, and (b) p = 1 and c = 2, (c) p = 0 and c = 0.2, and (d) p = 0 and c = 2. Other parameters are the same as in Figure 1.

Figure 3

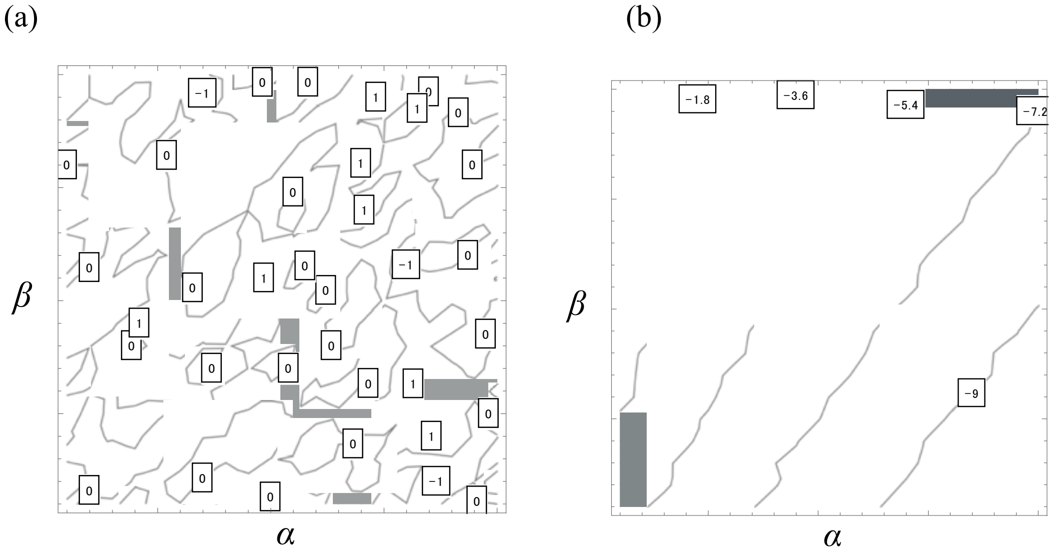
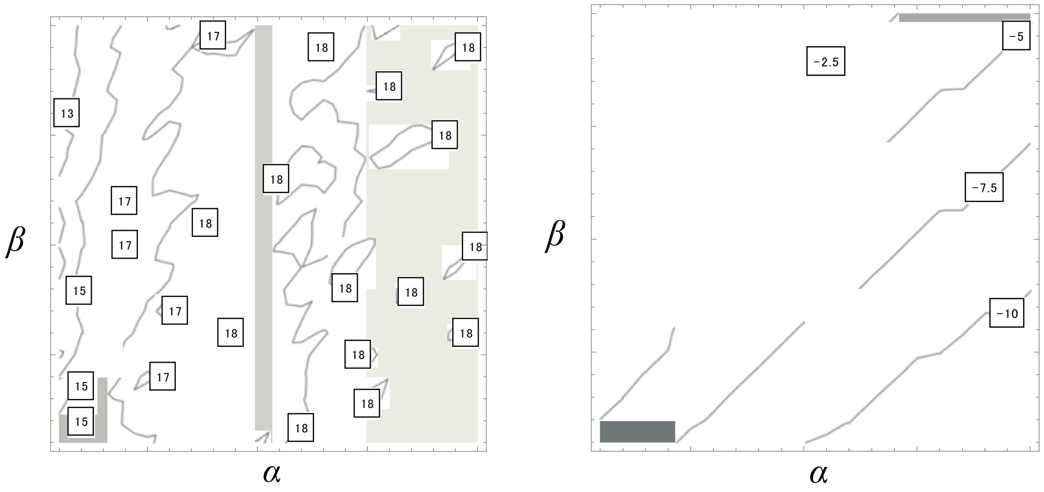


Figure 3. Score plot of each parameter set of the initial prior distribution for the intermediate p value. (a) $p = 0.5$, and (b) $p = 0.8$. Other parameters are the same as in Figure 1.

Figure 4


(a)

(b)

Figure 4. Cost dependence of the score plot for the intermediate p ($p = 0.8$). (a) $c = 0.2$, and (b) $c = 2$. Other parameters are the same as in Figure 1.

Figure 5

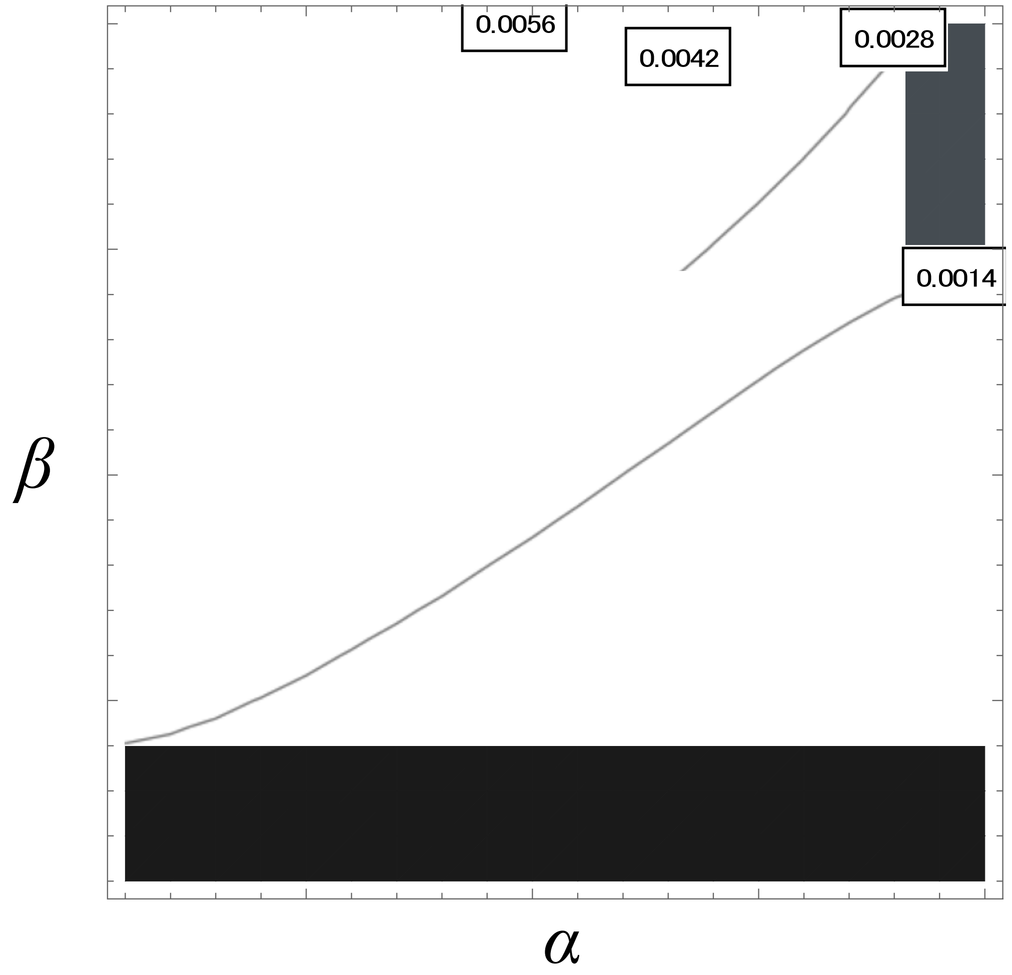


Figure 5. Figure of each strategy in the evolutionary endpoint. Parameters are; $b = 1$, $c = 1$, $N = 500$, $p = 0.8$, $M = 900$, $\mu = 0.01$, $W_0 = 100$.

Figure 6

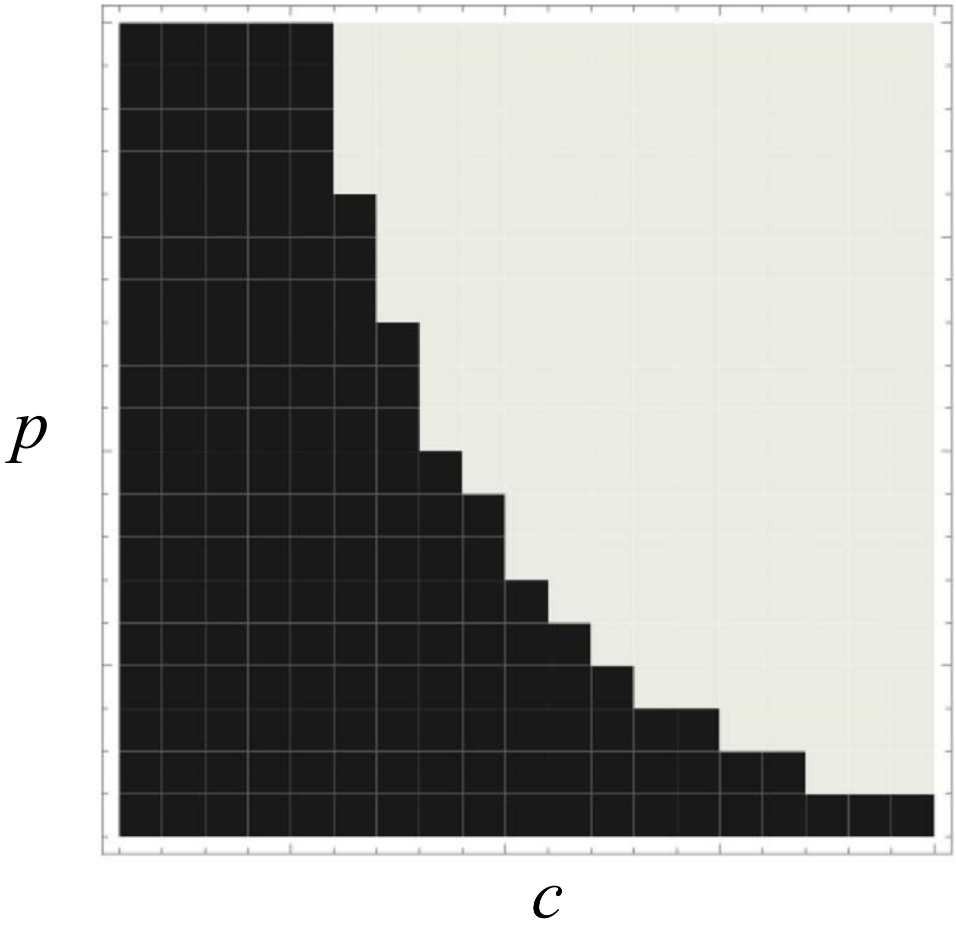


Figure 6. Condition at which predators should avoid prey items innately or by learning. Horizontal axis represents the cost of attacking unpalatable prey, *c*, and the vertical axis represents the frequency of unpalatable prey, *p*. The white area is where a predator should avoid signals innately. The black area is where a predator should avoid signals by learning. Parameters are the same as in Figure 5.

Acknowledgement

I gratefully acknowledge my adviser Professor Yoh Iwasa with the deepest appreciation for his advices on research. I would not complete my works without his support. I also thank to Professor Tom Sherratt. I learned a lot of things related to animal behavior from him. I also appreciate Akiko Satake, Shingo Iwami, Hiroshi Haeno, Toshiharu Akino, Masaru Hojo, Martin Stevens, Atushi Yamauchi, Koichi Ito, Karl Loeffler-Henry, Munetoshi Maruyama, Kazuki Tuji, John Wang, Hisashi Ohtsuki, Hiroto Shoji, Hiroyuki Shimoji, Andrew Higginson, Tim Fawcett, Shinji Nakaoka, Yoshifumi Yamawaki, Jenny Read, Ross Booton.

I would like to say big thank you to all the members of mathematical biology laboratory in Kyushu University: Yuya tachiki, Kenichi Hironaka, Koji Noshita, Nao Takashina, Ryosuke Iritani, Koki Uchinomiya, Marko Jusup, Ryo Yamaguchi, Kimiyo Yamamoto, Yuki Kubo, Douge Makoto, Jounghun Lee, Motohide Seki, Yusuke Ito, Shoya Iwanami, Akane Hara, Kosaku Kitagawa, Tatsuya Kurusu, Kengo Nagata, Junnosuke Horita, Mistuaki Takaki, Yuta Sawasaki, Yusuke Kakizoe.