Anti-predator strategy of frogs against snakes:
adaptive decision making for alternative use of fleeing and immobility

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Introduction

In anti-predator mechanisms, when the prey is located within the mutual perceptual field of prey and predator, prey responds by reducing the probability of successful predation. In this situation, prey animals often engage in secondary defense phase, which requires appropriate decision making of using anti-predator tactics. Most of cryptic prey animals are considered to use two types of anti-predator behavior as secondary defense; one is immobility, which is a motionless state of prey to enhance crypsis against visually hunting predators, and another is fleeing to increase distance from predator. In the present study, I focused on immobility and fleeing and conducted field and experimental studies to examine decision making for the use of these tactics in frogs, which are known to use immobility and fleeing against snakes to avoid predation. I considered two situations according to the status of predatory sequence: when snakes have not detected prey (Chapter 1) and when snakes have detected prey (Chapters 2 and 3). In both situations, I first experimentally examined how frogs switch these tactics. Then, I examined how the switching affects survival of
the frogs. Finally, based on the results of these experiments, I propose several factors that should be included in the future theoretical models of optimal anti-predator strategy.

Methods
The subjects are a ranid frog, *Pelophylax nigromaculatus*, and a colubrid snake, *Elaphe quadrivirgata*, both of which were collected from paddy field in Kyoto Prefecture, Japan. In Chapter 1, first I examined behavior of a frog that was introduced in an arena with a snake that has not detected the frog. I observed decision of the frog about choosing immobility or fleeing against the snake, focusing on distance between them. Then, I examined effectiveness of its decision. I observed predatory response of a snake against a frog in immobile or moving state at two different distances between them. In Chapter 2, I manipulated movement of a frog to induce a snake to detect the frog, and I examined behavior of the frog against the snake that has detected the frog. Then, I examined effectiveness of its decision by observing predatory response of a snake to immobile and moving frogs. In Chapter 3, I first examined duration of predatory event between frogs and snakes in nature. Then, I experimentally examined factors that affect successful escape of frogs in this duration, especially focusing on strike behavior of snakes in close quarters.

Results
In Chapter 1, frogs initially exhibited immobility, when snakes were moving at a long distance, and then switched from immobility to fleeing at a shorter distance even when snakes had not detected them. On the other hand, snakes at long
distance detected only fleeing frogs, whereas snakes at short distance detected both immobile and fleeing frogs. In Chapter 2, frogs exhibited immobility against a snake that has detected the frog. To the immobile frog, snakes approached more slowly than to the moving frog. In the situation of a single frog, snakes eventually reached the frog and struck it regardless of its behavioral state. However, in the situation of two frogs, the immobile frog survived because snakes are distracted to a moving frog. In Chapter 3, it was confirmed that the predation events between frogs and snakes are settled within a few seconds because there are refuges for frogs around the predation event. In the experiment, video analysis revealed that snakes are not able to change the trajectory of strike after initiating it and are not able to move in a split second after the strike behavior.

Discussion
Chapter 1 showed that the ability of snakes to detect motionless frogs depends on the distance, suggesting that the distance-dependent switching can be considered an adaptive strategy of the frog. However, a previous model predicts that cryptic prey should flee immediately on seeing a predator or not flee until being detected by the predator. To explain this discordance, I propose two new factors that affect the decision of switching from immobility to fleeing. In Chapter 2, it was demonstrated that even if immobility may lose its cryptic advantage when predator has detected the prey, immobility has another function of increasing latency of predator to attack. The increased latency heightens the probability of emergence of other prey within a perceptual area of predator, and then, immobile prey would be able to survive by distracting the predator to the
new prey. In Chapter 3, it was suggested that snakes are not able to move immediately after frogs evaded their strike movements. In addition, frogs are able to evade the strike of snakes at least with approximately 10 cm separation. Thus, keeping immobile to induce strike of snake would result in successful escape.

**Conclusion**

In theoretical biology, it has been assumed that the optimal timing of switching from immobility to fleeing should be triggered by the detection of predator. However, in the present study, it was demonstrated that timing of switching from immobility to fleeing does not necessarily depend on the detection of predator. Although the present study was conducted in a simplified environmental condition, and examinations in more natural setting would be required, I anticipate that incorporating findings in the present study will contribute to better understanding of the anti-predator strategy of animals in the real world.