Effects of attack direction of predators and modulation of escape trajectories by prey on the outcome of predator-prey interactions

捕食者の接近方向と餌生物の逃避方向調節が捕食-被食関係の成否に及ぼす影響

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Predator-prey interaction is a fundamental aspect of ecology because the outcome of the interaction determines population dynamics and life-history traits of both predator and prey. Prey uses various tactics to avoid being preyed upon by predators, and most prey species employ escape responses to avoid predation at the phase of the predator attack. Many studies have been conducted on escape responses in various species, and variabilities and modulations in the escape response parameters have been reported. However, the effects of variabilities and modulations on survival remain largely unclear, except for flight initiation distances. Here, I focused on two parameters: the predator's attack direction (i.e., the initial orientation of the prey relative to the predator) and escape trajectory. I examined how the parameters are variable and modulated depending on the situation and how these variabilities and modulations affect the outcome of predator-prey interactions through the following three experiments.

Generally, the escape probability increases in response to the increase of flight initiation distance of prey. The initial orientation of the prey may affect the flight initiation distance through the bias in the sensory perception range of prey. Here, I recorded the escape responses of juvenile red sea bream (*Pagrus major*) to the predatory scorpion fish (*Sebastiscus marmoratus*) in an aquarium setting (Chapter 2). Flight initiation distance tended to be small when prey were attacked from behind, suggesting that prey have spatial bias in detecting attacking predators. An increase in flight initiation distance increased escape probability. An increase in the initial orientation (i.e., prey is attacked from behind) decreased turn duration and increased escape probability when the effect of flight initiation distance was offset. These results suggest that initial orientation affects escape probability through two different pathways: changes in flight initiation distance and turn duration.

Most previous studies have used a single threat or model predator as a stimulus. In nature, however, multiple predators may attack from different directions simultaneously or in close succession. It is unknown whether prey are able to change the escape trajectory when startled by multiple stimuli at various time intervals. Here, Pacific staghorn (*Leptocottus armatus*) were startled with a left and right visual stimulus in close succession (Chapter 3). By varying the timing of the second stimulus, I was able to determine when and how a second stimulus could affect the escape trajectory. Four treatments were used: a single visual stimulus (control); or two stimuli coming from opposite sides separated by a 0 ms (simultaneous treatment); a 33 ms; or a 83 ms time interval. The 33 ms and 83 ms time intervals were chosen to occur shortly before and after a predicted 60 ms visual escape latency, which is a required time interval to initiate their body motion. The 0 ms and 33 ms treatments influenced both the escape trajectory and the turning angle, compared to a single stimulation, whereas the 83 ms treatment had no effect on the escape response. I conclude that Pacific staghorn sculpin can modulate their escape response only between stimulation and the onset of the response, but that escape responses are ballistic after the body motion has started.

The escape trajectory can be modulated according to the change in the surrounding environment (e.g., sounds), even when the environmental change alone does not elicit escape responses. For example, crickets (*Gryllus bimaculatus*) modulate wind-elicited escape behavior depending on the acoustic context, where crickets exposed to 15 kHz tone escape backward more frequently than those without sounds. To clarify the adaptive significance of the modulation in escape trajectory, I conducted a virtual predator-prey experiment on a computer to simulate the outcome of the predator-prey interaction, using the previously published escape behavior of crickets (Chapter 4). I then investigated whether the escape trajectory affects the escape probability. The escape probability was higher in crickets moving backward than those moving forward, and the escape probability was higher in the treatment exposed to 15 kHz tone than that in control. These results suggest that crickets modulate escape trajectory to move backward because the environment with 15 kHz tone is more dangerous for crickets, and escaping backward is more effective for escaping from predators.

These findings indicate that variabilities and modulations of the initial orientation and escape trajectory affect escape probability, and provide the basis for further investigation in other prey species. Our finding that initial orientation affects escape probability through two different pathways highlight the importance of incorporating initial orientation into other studies of the kinematics of predator-prey interactions. The finding that prey fish can modulate their escape response only between stimulation and the onset of the response is of great importance not only from the viewpoint of ethology but also from the viewpoint of neurophysiology. The virtual predator-prey experimental system developed in this study can be applied to predator-prey interactions of various species to evaluate the adaptive significance of the observed escape behaviors without lethal consequences to the prey.