論 文 の 内 容 の 要 旨

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平成２１年度博士課程　入学
氏　　　名　塩見 こずえ
指導教員名　佐藤 克文

論文題目　Decision Time to Return in Seabirds: application of fine-scale movement data to decision-making analyses
（高精度移動データに基づく海鳥の意思決定分析）

Animals move to search for resources (e.g. prey, mate, refuge) and to escape stress sources (e.g. predator, inter-species competition). Because the distribution of these external factors and/or animals' internal conditions can change heterogeneously in time, timing of movements is essential for efficient use of the resources and for avoidance of unfavorable situations. In the past, timing of movements between fixed two sites, such as seasonal migration between breeding and overwintering areas, has been well studied in relation of environmental changes with circadian, circannual, and tidal rhythms. However, timing behaviors in more variable situations have little investigated. It is partly because, if sites of departures and arrivals are not fixed and range beyond our observable area, recording of timing of the movements is almost impossible. Recently, miniaturized animal-borne data loggers enable us to obtain fine-scale movement paths of free-ranging animals remotely and continuously. This method should be useful to investigate flexible movements in the wild.

Seabirds perform central place foraging, which is defined as a set of departure from a place ('central place'; e.g. nest and roost), foraging at distant sites, and return to the same place again. Because distribution of their prey at sea is often dynamic, seabirds' movements to search for the prey and the consequent foraging sites are also variable. The need to return may constrain their behavioral range and trip duration, but more than that, the central place could have significance, for example, as breeding and resting sites. Under the presence of the trade-off, decision on when to return the central place appears important in the coordination of their trips. In this thesis, using fine-scale movement paths of seabirds recorded by animal-borne loggers, when to start returning is investigated in two different kinds of central place foraging: diving under the water and flying over the sea. As model species, diving emperor penguins *Aptenodytes forsteri* and flying streaked shearwaters *Calonectris leucomelas* are selected.

Emperor penguins: model species of diving seabirds

Emperor penguins are the largest species in the family Spheniscidae. They breed in austral winter on the fast sea ice around Antarctic continent and perform foraging trips at sea. During the trips, they repeat dives not only for foraging but also for horizontal travelling. Emperor penguins have the greatest diving ability among the avian group, of which the deepest record of dive depth was 565 m, and the longest dive duration was 27.6 min.

At some point in a dive, breath-hold divers must decide to return to the surface to breathe. The water surface can be considered as a central place for divers. Longer stay underwater could provide more prey or increase distance traveled, but might also require longer recovery times at the surface as well. In this context, the issue of when to end a dive has been discussed intensively in terms of foraging ecology and diving physiology, using dive duration as a temporal parameter. Inevitably, however, a time lag necessarily exists between the decision of animals to start returning to the surface and the end of the dive, especially in deep dives. Therefore, we examined not dive duration but the decision time to return in emperor penguins by analyzing three-dimensional dive paths. So far, no study has reconstructed fine-scale 3-D dive paths of avian species. Experiments were conducted under two different conditions: during foraging trips at sea and during dives in semi-captive conditions, where penguins dived through an artificial ice hole in an enclosure. It was found that there was an upper limit for the decision-to-return time irrespective of dive depth in birds diving at sea. However, in a large proportion of dives performed by the semi-captive birds, the decision-to-return time exceeded the upper limit at sea. This difference between the decision times in the two conditions was accounted for by a difference in stroke rate. The stroke rates, which were counted from acceleration data, were much lower in dives in the semi-captive conditions and were inversely correlated with the upper limit of decision times in individual birds. Unlike the decision time to start returning, the cumulative number of strokes at the decision time fell within a similar range in the two experiments. This finding suggests that the number of strokes, but not elapsed time, constrained the decision of emperor penguins to return to the surface. While the decision to return and to end a dive may be determined by a variety of ecological, behavioral and physiological factors, the upper limit to that decision time may be related to cumulative muscle workload.

Streaked shearwaters: model species of flying seabirds

Streaked shearwaters are pelagic seabirds in the family Procellariidae. They breed in east and Southeast Asia, mainly in Japan and Korea, nesting underground at islands. During chick-rearing period, they repeatedly commute to the sea for foraging and return to the island to feed their chick as typical central place foragers.

In the foraging trips of some seabird species including streaked shearwaters, while foraging areas disperse widely up to several hundred kilometers from the nesting colony, arrival times at their colonies concentrate within several hours after sunset. This temporal pattern raises the question of how they manage to time arrivals over largely variable homeward distances. However, no study has investigated their at-sea behavioral patterns associated with arrival times. To explore this question, we tracked breeding streaked shearwaters with GPS data loggers, which continuously recorded fine-scale movement paths during their trips. Their foraging areas in long trips varied from 96 km to 457 km in the distance from their colonies. Shearwaters adjusted the onset of their homeward journeys according to the wide-ranging distances between their chosen foraging areas and breeding colonies, leaving earlier from further locations. In the farthest trip, the bird left early in the morning, while in the nearest one, homing started a few hours before sunset. The start time of homing was pushed forward correlating with the increased travel time expected from their homeward distance and average movement speed. This resulted in arrivals at the colony concentrated within a few hours after sunset independent of the distances. To our knowledge, similar temporal tuning of homing trips has not been reported previously in non-human animals. The strong correlation between the timing and distance of homeward journeys implies the compromise between the demand for foraging at sea and the need to arrive at the colony within a specific time window. Their night arrival has been ascribed to the presence of diurnal predators such as raptors, and a previous study on a related species, Manx shearwaters, suggested that the concentration of arrivals after sunset reflect navigational mechanisms depending on diurnal cues such as sun. Thus, streaked shearwaters appeared to time homing trips to overcome several constraints at the same time.

Comparative discussion

Both of the two species did not change moving speeds depending on the distances to their central places: in emperor penguins, mean swim speeds to the surface distributed around 2.1 m s^{-1}, and in streaked shearwaters, around 9.6 m s^{-1}. Biomechanical models predict that cost of traveling (J m^{-1}) in fluid depends on moving speed and that the speed minimizing the cost is independent of traveled distances. The empirical ranges of moving speeds were consistent with the cost-minimizing speeds estimated by the model. Thus, moving speeds appeared to be constrained by cost efficiency.

As the onset time and speeds of movements are the main determinant of arrival times, given that speeds should not be changed, the importance of the timing to start returning would become increasingly evident. The fine-scale movement paths of diving emperor penguins and flying streaked shearwaters indicated that there were some tendencies in the timing of the decision to start returning. In the penguins, the upper limit of the time to start returning was related to muscle workload, i.e. a physiological factor. This seems reasonable for breath-holding divers because deciding too late at depth would lead directly to death. In the shearwaters, on the other hand, the onset of homeward trips was adjusted according to changes of travel time expected from their flight performance. This could be an adaptation to the combination of dynamic prey distribution and the constraint on arrival times. The timing of the decision to return in shearwaters was likely to relate to the predator avoidance and navigational mechanism, i.e. ecological and cognitive factors. Comparison of the two seabird species under the different situations revealed that timing to start returning could be affected by several kinds of constraints. Considering they travelled in natural environments, where many potential factors may affect their movements, the decision rules found under such complicated conditions should have a great significance for their survival. Novel analyses of fine-scale movement data indicated that seabirds timed their inward movements according to variable situations and that timing ability for the onset to return is the key to solve the trade-off in central place foraging.