OPINION

Opinion is intended to facilitate communication between reader and author and reader and reader. Comments, viewpoints or suggestions arising from published papers are welcome. Discussion and debate about important issues in ecology, e.g. theory or terminology, may also be included. Contributions should be as precise as possible and references should be kept to a minimum. A summary is not required.

Measuring diving success of otters

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Recently, Kruuk et al. (1990) reported on the foraging behavior of otters (*Lutra lutra*) in a marine environment in Shetland. Kruuk et al. noticed that otters tended to concentrate their hunting dives in certain "patches", and the authors evaluated several potential alternative causes of "patch-fishing". Kruuk et al. presented evidence against the hypotheses that patches contained higher densities of prey (fishes) or were closer to shore features, such as holts and landing sites. Perhaps most surprisingly, they demonstrated that otters were equally as successful hunting outside patches as they were hunting in them. They concluded that the feeding patches were characterized by greater linear distances of edge between kelp (*Laminaria*) and open water, and these edge-rich areas allowed the otters easier access to the benthos, where fish lurk. They interpreted the lack of higher success rates in these edge-rich patches as being the result of otters choosing to dive in spots having "some predetermined probability of success" (p. 71). Some stretches of shoreline ("patches") were dived in more frequently simply because they had more of these spots. Thus, according to Kruuk et al., otters do not dive "blind", but ostensibly are aware of the probability that the dive they are about to undertake will be successful. Since that probability is based on the location of the dive, otters simply choose to dive in only those locations having the highest probability of success and ignore others. This would explain their constant success rate (about 25%) inside and outside patches.

Since "success", defined as percentage of dives (or hunts) in which prey are obtained, did not, in their study, seem to reflect prey abundance, predator efficacy, or habitat suitability, Kruuk et al. suggested that alternative definitions be substituted in future studies of carnivore foraging. In particular, they contended that "an individual dive (or any other single prey-catching attempt) is for many purposes not a suitable unit of prey-catching effort, despite its general use." (p. 71). I argue here that it is premature to abandon the use of prey captured per dive (or hunt) as a measure of hunting success in otters (or other Carnivora). My arguments are based on studies of two other species of otter that forage in marine environments: the sea otter (*Enhydra lutris*) and the marine otter (*Lutra felina*). In these species, percentage of dives that are successful varies with prey type, hunting tactics, and locality. Although the causes of variation in hunting success thus measured are not always well understood, I believe that useful insights are still obtainable with this method.

Success rate is related to prey type

Estes et al. (1981) categorized individual Aleutian Islands sea otters as "fisheaters" or "non-fisheaters" on the basis of prey chosen during single foraging bouts (a series of foraging dives over a period up to several hours). They found that fisheaters were successful on 86.0% of their dives, whereas non-fisheaters (which ate mostly sea urchins) were successful 94.3% of the time, a significant difference. Estes et al. (1981) postulated that the two types of strategies involved search images for each prey type. Since fish are less abundant and more elusive than sea urchins, otters searching for fish are less likely to be successful on any given dive. Similarly, some otters in Prince William Sound, Alaska forage principally on clams, whereas others concentrate on mussels. The former were successful 75.5% of the time whereas the latter were successful on 98.7% of their dives (Estes et al. 1981). Clams at this locality occur under soft sediment and must be dug out. Their capture probability may be more uncertain, or successful capture may require > 1 dive. Success rates therefore reflect tactics of prey selection by foraging otters.

Success rate is related to dietary switching

Sea otters often have an impact on their prey communities by depleting certain prey species (Estes and Palmisano 1974, Ostfeld 1982). In California, otters often change their diet after the first several months or years after repopulating an area and begin to include less profitable species (Ostfeld 1982), a process that coincides with changes in success rate. For example, when otters first reoccupied the kelp forests off Santa Cruz, California in 1977, they frequently took sea urchins and were successful on about 35% of their foraging dives. After sea urchins were depleted, the otters switched to clams and their success rate increased dramatically (about 57% of dives successful). It is plausible that poor success rates while hunting for diminishing numbers of sea urchins induced otters to switch to more abundant (but less profitable) prey (Ostfeld 1982).

Individual sea otters tend to focus on one particular prey type during any given foraging bout, but there is evidence that unsuccessful dives induce them to abandon one prey type for another. For instance, Estes et al. (1981: 626) found that "prey switching was significantly more frequent for pairs of successful dives separated by 1 or more unsuccessful dives than it was for 2 successful dives in sequence ..." In addition, Ostfeld (1982) found that on average 0.7 unsuccessful dives separated successive captures of the same prey type ("not switching"), whereas 2.0 unsuccessful dives separated successive captures of different prey types (switching), a significant difference. Thus, in many instances, probability of success is not a fixed term, but rather fluctuates continuously depending on prey type, and appears to be monitored by foraging otters.

Success rate is sometimes related to time spent foraging

Success rates of foraging marine otters varied dramatically among three study sites in Chile (Ostfeld et al. 1989). At a northern and southern site success rates were 37.3% and 37.8%, respectively, whereas at a central site it was 15.8%. Otters at the central site spent about twice as much of their daylight time foraging (ca. 40%) as the otters at the two other sites (10–20%), which may have been necessitated by their poor success rate (Ostfeld et al. 1989). Thus, success rate may be an important determinant of daily activity budget in this species.

Success rates for *E. lutris* also vary considerably among locations, but in this species the variation is not related to time spent foraging. For instance, otters at Amchitka Island and Attu Island (western Aleutian Islands) were successful on 92.2% and 94.0% of their dives, respectively, but they spent ca. 55% and 16%, respectively, of their daylight hours foraging (Estes et al. 1982). Estes et al. (1981: 618) found that success rate was "remarkably invariant among study locations within geographical areas, despite the fact that these areas supported sea otter populations of varying status." They concluded that the abundance or biomass of prey was not important in determining success rate, an interpretation that seems consistent with Kruuk et al. (1990). However, vastly different success rates among localities may indicate that success rates measure something of importance about the otters' community.

Success rate may reflect prey community organization

Although otters in the Aleutian Islands successfully procured prey on > 90% of their dives, those in Prince William Sound and California were successful only on about 80% and 70% of their dives, respectively (Estes et al. 1981). At another California site, success rates were as low as 35–40% (Ostfeld 1982). Therefore, even if success rate "merely measure[s] the likelihood that a predator will initiate a hunt after observing a situation with the potential for a capture" (Kruuk et al. 1990: 71), this may be a meaningful reflection of habitat quality or foraging strategy.

If success rate is not determined by prey abundance or biomass, it may instead reflect selectivity by otters. Otters in California and Prince William Sound may be more likely to continue searching even after locating an individual prey, in order to procure a higher quality prey. If a more suitable prey item is not located within a certain length of time underwater, the otter surfaces and dives again. Why there should be geographical differences in searching strategies, if indeed there are, is not entirely clear. Perhaps prey are more patchily distributed in Prince William Sound and California than in the Aleutians, leading to a low mean and high variance in the probability that a high quality prey item will be encountered on any particular dive.

Diving success and foraging strategies

Why do Shetland otters have a constant foraging success rate when other, ecologically similar species have varying success rates in space and time? *Lutra lutra* in Shetland feed almost entirely on fishes (Kruuk and Moorhouse 1990), and the generally high mobility of these prey may result in their rapid replacement after otter foraging bouts (Kruuk et al. 1988). This would cause diving success rates to be predictable within patches, as has been discovered by Kruuk et al. (1990). In contrast, other marine-dwelling otters tend to specialize on invertebrate prey (Estes 1989, Ostfeld et al. 1989). Low mobility of prey such as sea urchins, molluscs, and to a lesser extent, crustaceans, may reduce their replacement rates and allow foraging patches to become depleted temporarily or permanently. If so, then these otters may not possess information that allows them to choose diving sites according to predictable patch-specific probability of success.

Another possible cause for the differences between species concerns dietary breadth. The marine fishes on which *L. lutra* prey are ecologically similar to each other (Kruuk et al. 1988), and it may be that the otters employ a single foraging strategy (e.g., decision rule for patch selection, or search image) that is equally effective for all prey types. Hence, success rates are quite similar among sites. For other marine-dwelling otters, their diverse assemblage of invertebrate and fish prey may require several different foraging strategies and greater behavioral flexibility (Estes et al. 1981, Ostfeld 1982). Thus, varying success rates may be both a cause and consequence of a constantly changing diet.

In conclusion, foraging success, as measured by percent of hunting dives (or events) successful, is a complex and enigmatic issue. Kruuk et al. (1990) have rightfully emphasized the need for great care in applying this concept in field studies. But the studies reviewed above indicate that it still may be a useful means of comparing foraging strategies and habitat characteristics among and within populations of carnivores.

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References

Estes, J. A. 1989. Adaptations for aquatic living by carnivores. – In: Gittleman, J. L. (ed.), Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, NY, pp. 242–282.

– and Palmisano, J. F. 1974. Sea otters: their role in structuring nearshore communities. – Science 185: 1058–1060.

– , Jameson, R. J. and Johnson, A. M. 1981. Food selection and some foraging tactics of sea otters. – In: Chapman, J. A. and Pursley, D. (eds), The worldwide furbearer conference proceedings. Worldwide Furbearers Conference, Inc., Frostburg, MD, pp. 606–641.

– , Jameson, R. J. and Rhode, E. B. 1982. Activity and prey selection in the sea otter: influence of population status on community structure. – Am. Nat. 120: 242–258.

– , Underwood, K. E. and Karmann, M. J. 1986. Activity-time budgets of sea otters in California. – J. Wildl. Manage. 50: 626–636.

Kruuk, H., and Moorhouse, A. 1990. Seasonal and spatial differences in food selection by otters (*Lutra lutra* L.) in Shetland. – J. Zool. Lond. 221: 621–637.

– , Nolet, B. and French, D. 1988. Fluctuations in numbers and activity of inshore demersal fishes in Shetland. – J. mar. biol. Ass. U. K. 68: 601–617.

– , Wansink, D. and Moorhouse, A. 1990. Feeding patches and diving success of otters, *Lutra lutra*, in Shetland. – Oikos 57: 68–72.

Ostfeld, R. S. 1982. Foraging strategies and prey switching in the California sea otter. – Oecologia (Berl.) 53: 170–178.

– , Ebensperger, L., Klosterman, L. L. and Castilla, J. C. 1989. Foraging, activity budget, and social behavior of the South American marine otter *Lutra felina* (Molina 1782). – Nat. Geogr. Res. 5: 422–438.