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GENERAL BIOLOGY

Experimental Study of Cognitive Aspects of Ambivalent Foraging as Exemplified by the Great Tit

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Abstract—A hypothesis of ambivalent foraging is proposed based on ideas about dual treating of the prey by a consumer: the food value attracts while the danger repulses. The foraging strategy of the great tit was investigated experimentally with the use of artificial "food patches" with variable amounts of dangerous prey (live red wood ants) and non-dangerous prey (fly larvae). With non-dangerous prey, the behavior of the birds corresponded to the known marginal value theorem: they proceeded with foraging until the resources were exhausted. We found the threshold amount of dangerous prey that prevents tits from hunting.

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The behavior of consumers in the behavioral ecology is traditionally described on the basis of the concept of optimal foraging: for "decision-making," animals compare the energy costs of obtaining and handling of the prey and the resulting energy gain. Determination of the marginal value of the "food patch" [1] can be facilitated by cognitive resources. For many species, from lizards to primates, the ability to estimate the relative number of objects and to choose the larger amount of prey has been demonstrated [2]. Models of risk-sensitive foraging consider the possible risks that can occur when obtaining food: situations related to the depletion of food resources, as well as the depletion of internal resources of the consumer [3, 4]. Risks associated with the prey as a source of danger have been studied only for a few situations, such as with meerkats hunting scorpions [5]. We found a successful behavioral model for the interaction of small vertebrate animals with dangerous prey based on facultative foraging and requiring flexible behavior by the consumer: the hunting of small rodents for red wood ants, which represent a high nutritional and hedonistic value for them [6]. In this situation, the consumer cannot just choose based on a higher number of prey; it should assess the marginal value of the abundance of the prey, which allows safe consumption. The behavioral and evolutionary ecologies require a new approach to the study of such relationships. We propose the hypothesis of ambivalent feeding based on ideas about dual treating of the prey by a consumer: food value is attractive while danger is repulsive. We assume that the animals have to assess not only the nutritional value, but also the danger marginal value and thus a "reasonable violation" of the rules of optimal foraging, choosing a smaller rather than larger amount of prey. This ability was first experimentally demonstrated for striped field mice that prey on red wood ants, which consistently selected lesser amounts of dangerous prey [6].

Here, we report the results of the first experimental studies on the interaction of the great tit *Parus major* with red wood ants *Formica aquilonia*, which have allowed us to develop the concept of ambivalent feeding. Some aspects of adverse interactions of these species [7] and the high aggressiveness of ants [8] have been demonstrated previously.

In the study, we used tits caught in the park area of Novosibirsk. The tits were kept in cages with removable sections (two cubes with sides of 15 cm) attached to the front side of the cadge. In the residential section, the tits received food and water between experiments, the removable sections were used to produce artificial "food patches": sets of dangerous prey (ants) or safe prey (dyed fly larvae of family Calliphoridae). The tits were free to enter both sections during the 15-min test. The behavior of the tits was recorded with a video camera and analyzed manually by means of a VLC media player using the slow motion playback option.

In tests with dangerous prey, each of seven tits was offered a choice of two "food patches" with 10 and 15 ants (14 tests, 5 h of video material), varying sides (right or left) in random order. During the processing of the recorded material the duration of the assessment of the situation by the bird, the duration of the

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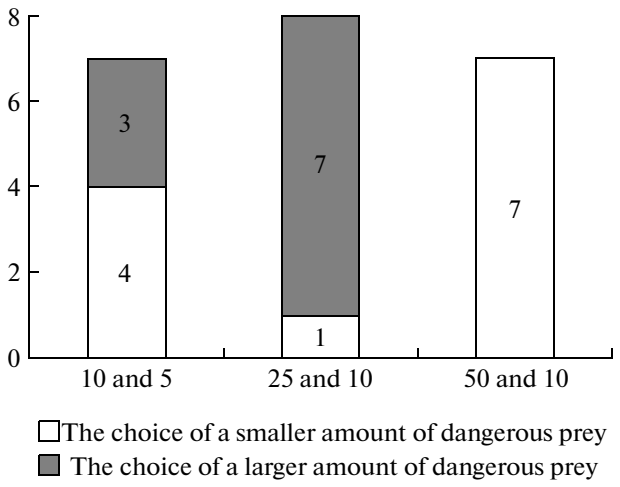
hunting and attempts to leave the "food patch" were fixed. In tests with non-dangerous prey, four tits were offered a choice between four fly larvae at ratios of 3 : 6 and 10 : 15. Empty "food patches" were offered in the control tests.

The abilities of tits to assess the amount of dangerous prey were investigated in a transparent arena (57 × 39 × 28 cm), divided with a removable partition on the "input" and "working" parts. In the "working" part ants were placed in two feeders in ratios of 5 : 10, 25 : 10, and 50 : 10 in different tests. At the beginning of the test, a tit was placed in the "input" part of the arena, where it could estimate the amount of dangerous prey in the feeders for 60 s through the transparent partition, after it had access to the "working" part of the arena, where one of the two feeders with dangerous prey in could be opened. The test was terminated 20 min after the start, or earlier if the tit accidentally opened the feeder (with a wing, foot, or air currents). Only in tests where the bird opened the feeder by pecking on the lid with its beak were statistically processed. In total, 74 experiments with five tits were performed (more than 20 h of video recordings).

Upon presentation of the non-dangerous prey, the behavior of tits was in line with marginal value theorem [1]: once the tits were in the removable section, they remained there until they could find the prey, after which they moved to the next "food patch." In control experiments with an empty "food patch," the tits, after evaluating the situation (for up to 10 s) left the section, and, after three to five repeated visits, they lost interest in the empty "patch" until the end of the experiment.

In a series of tests with dangerous prey, we found that tits efficiently hunt and eat the prey if there were 6–10 ants per patch, remaining at the "patch" for 4.9 ± 0.7 s. The behavioral sequence of the bird included behavior elements of hunting and handling of the prey. For smaller amounts of ants (1–5), the average duration of the behavioral sequence was 5.3 ± 0.8 s, and the bird can hunt and handle the prey. With large quantities of ants (11–15), the tit cannot effectively hunt or eat the prey. The average duration of the behavioral sequence is significantly reduced to 2.3 ± 0.3 s ($p < 0.05$, Pearson's test). According to our observations, this is due to the fact that tits hunt "on impulse" with such an abundance of ants: the duration of each individual behavioral sequence is shorter, because the danger posed by the ants does not allow a longer stay in the "food patch." As in the case of striped field mice in similar experiments [6], for large quantities of dangerous prey, tits are not always immediately ready for handling the prey after immobilizing an ant. They first kill and then leave the dangerous insect. With a decrease in the number of live ants, the risk reduces, and, at a certain amount of ants (6–10), the bird starts to eat them directly during the hunt, and then picks up and eats the ants killed earlier. Some birds moved the ants caught in a relatively quiet place, and there handle and eat the prey.



The ratio of choices (the vertical axis) of larger and smaller amounts of dangerous prey (red wood ants) made by tits.

Evaluation of the ability of tits to estimate the amount of dangerous prey has shown that their behavior corresponds to our ambivalent foraging hypothesis. The choice between 5 and 10 ants did not differ from random selection ($p > 0.05$, Pearson's test). The significantly frequent choice of higher amounts in the second series of tests (choice between 25 and 10, $p < 0.05$, Pearson's test) means that 25 ants are not significantly dangerous for the tits, and they are a valuable food resource. For the ratio of ants of 50 : 10, the tits chose the smaller amounts in 100% of cases, which indicates the cognitive capacity of allowing to assess the risk (figure). It should be noted that only in the first and second series of tests did the tits often open the second feeder as well. This is easy to explain. In the first series, none of the "food patches" represent a real danger. In the second series the dangerous "food patch" was already open, and there was no reason not to visit the less dangerous "food patch." In the third series, the tits, after assessing the situation, did not open the dangerous feeder.

Thus, there are reasons to consider ambivalent foraging as one of the foraging strategies of animals. We assume that the cognitive ability of tits to perform risk assessment based on the proportion of dangerous prey is the basis of ambivalent foraging.

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