

MOTIVATION AND MEASURES OF ACCESSIBILITY¹

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Food accessibility in the arboreal environment typically has been investigated with reference to the morphological characteristics of the species concerned (e.g., Newton 1967; Partridge 1976a, 1976b; Denslow and Moermond 1982; Moermond and Denslow 1983, 1985; Moermond and Howe 1986). While acknowledging the role which morphology plays in determining limits of accessibility, it should be recognized that measures of accessibility are necessarily made up of two components: (1) the ability to reach and (2) the motivation to reach. Thus, measures of accessibility must be, in part, a function of energetic state. This prediction arises from simple cost/benefit reasoning. Obtaining difficult-to-reach prey items must entail some cost, the most obvious being the energy expended to obtain the item. Other costs may include injury, resulting from a fall or perch breakage, or simply reduced awareness of surrounding stimuli, such as the approach of a predator. While such costs may or may not be state-dependent, the benefit of obtaining a particular prey item does depend on the energetic state of the organism, because the marginal value of a unit of energy is greater to an organism with low energetic reserves than a similar organism with higher reserves. For example, McNamara and Houston (1990) determined theoretically that the probability a forager dies of starvation is approximately an exponential function of the size of its energetic reserve. Hence, a bird with low energetic reserves should be more willing to pay the costs of obtaining a difficult-to-reach prey item than a bird with higher energetic reserves (because its net gain would be greater). This reasoning is analogous to that of the more familiar trade-offs between starvation and predation risk (e.g., Pulliam et al. 1982, Lima 1987, McNamara and Houston 1987, McNamara 1990) or collision risk in flight (Cuthill and Guilford 1990).

Previous studies illustrated the dual importance of state and morphology in determining the handling time of prey items. For example, handling time varies with period of food deprivation and perceived predation risk (for a review, see Lima and Dill 1990). Handling time is additionally known to be a function of bill dimension and shape (e.g., Gosler 1987a, Benkman and Lindholm 1991, Cuthill et al. 1992). I investigate here the proposition that measures of food accessibility, like handling times, are a function of energetic state. This hypothesis is tested in four distinct foraging tasks

performed during arboreal foraging in the European Starling, *Sturnus vulgaris* (see Feare 1984, Snow and Snow 1988): (1) reaching out, (2) reaching down, (3) reaching up, all from a fixed perch, and (4) reaching to the end of a flexible perch. State was manipulated in two distinct ways: (a) providing two different numbers of prey items, immediately before the trial, following a single deprivation time, and (b) administering two different deprivation times prior to the experimental trial. The possible confounding effect of change in body mass is examined. Finally, the relevance of these results for previous measures of accessibility is considered.

METHOD

The experiment was carried out on nine wild-caught adult European Starlings, seven males and two females, which were housed individually in $0.5 \times 0.3 \times 0.3$ m cages. Birds were maintained at a constant temperature of 20°C on a 13L:11D photoperiod preceding and throughout the experiment. Turkey crumbs and water were available *ad libitum*, except as described below, and mealworms (*Tenebrio* larvae) were provided every other day, except on the day preceding, and of, the experimental trials. Foraging tests were carried out in a $1 \times 1 \times 1$ m cage.

Prior to foraging trial 1, all nine birds experienced a 120 min food deprivation. Immediately preceding the trial, five birds each received five mealworms ("low deprivation"), the remaining four birds received one mealworm ("high deprivation"). Each bird was individually transferred to the test cage, which contained a single fixed perch (diameter 0.006 m) and a mealworm suspended from a retort stand 0.135 m away at the same level as the perch. The bird's activities were recorded on video, over a 10 min period, for subsequent analysis. Birds from "low deprivation" and "high deprivation" treatment groups were tested alternately. The following day the deprivation treatment of each bird was reversed and birds were retested in the same order as day 1.

Prior to foraging trial 2, five of the birds experienced a 120 min food deprivation ("high deprivation") and the remaining birds experienced a 30 min food deprivation ("low deprivation"). In this trial, the birds had to reach down (0.066 m) and outwards (0.101 m), a diagonal distance of 0.121 m, in order to reach the mealworm. The activities of each bird were again recorded on video. Tests of "high deprivation" and "low deprivation" birds were alternated. The following day, the deprivation treatment for each bird was reversed and the birds were retested, in the same order as the previous day.

The treatments and procedures in trial 3 were iden-

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TABLE 1. The mean (SE, where appropriate) values of "success" (number of mealworms taken), distance reached from, or along, the perch (cm), number of attempts and, for trial 4, handling time (sec) for each treatment group. Note that sample sizes for "distance" vary because birds which made no attempt to obtain the mealworm were excluded from the analysis. Sample sizes for "distance" are as follows: Trial 1, $n = 7$; Trial 2, $n = 6$; Trial 3, $n = 8$; Trial 4, $n = 9$. For "handling time," $n = 7$. In all other cases, $n = 9$. Apparent discrepancies between sample sizes and degrees of freedom for "distance" are the result of identical paired values. See text for details of the experimental trials and statistical tests employed.

| | High deprivation | | Low deprivation | | df | P |
|---------------|------------------|------|-----------------|------|----|-------|
| | \bar{x} | SE | \bar{x} | SE | | |
| Trial 1 | | | | | | |
| Success | 8 | | 1 | | 1 | 0.008 |
| Distance | 13.5 | 0.00 | 12.4 | 0.44 | 6 | 0.036 |
| Attempts | 1.55 | 0.48 | 1.44 | 0.38 | 8 | 1.000 |
| Trial 2 | | | | | | |
| Success | 7 | | 1 | | 1 | 0.031 |
| Distance | 11.8 | 0.17 | 10.8 | 0.67 | 3 | 0.181 |
| Attempts | 2.22 | 0.57 | 2.00 | 0.68 | 8 | 0.859 |
| Trial 3 | | | | | | |
| Success | 5 | | 4 | | 1 | 1.000 |
| Distance | 7.78 | 0.64 | 6.26 | 0.52 | 4 | 0.800 |
| Attempts | 1.89 | 0.69 | 1.56 | 0.39 | 8 | 0.753 |
| Trial 4 | | | | | | |
| Success | 9 | | 7 | | 1 | 0.500 |
| Distance | 12.9 | 0.00 | 12.5 | 0.33 | 2 | 0.371 |
| Attempts | 1.56 | 0.24 | 2.00 | 0.50 | 8 | 0.295 |
| Handling time | 1.76 | 0.23 | 2.23 | 0.26 | 6 | 0.022 |

tical to trial 1, except that, in this case, the birds had to reach to the end of a highly flexible plastic perch (diameter 0.01 m), 0.15 m long, in order to obtain the mealworm, which was attached at the end of the perch. Birds were free to move along the length of this perch. In trial 4, the procedure was identical to trial 2, but the foraging task involved reaching above (0.08 m) and away (0.101 m) from the perch, a diagonal distance of 0.129 m.

Each of the foraging trials was separated by two days. The variables measured subsequently from video tape, for all of the above trials, were "success" (whether or not the mealworm was taken), the number of attempts to obtain the mealworm, handling time and the maximum distance reached away from the perch (trials 1, 2 and 4), or the maximum distance moved along the perch (trial 3).

The distances used in the above foraging tasks were determined from pre-experimental trials, on different birds, and were designed to be near to the apparent reaching limits of the birds under these circumstances. Although experimental birds were familiar with the process of obtaining mealworms in the test cage, they were naive to these specific tasks.

In a separate procedure, I measured the effect of the food deprivations, used in trials 2 and 4, on body mass in 12 birds, different from those used above, housed under identical conditions. Half of the birds experienced a 30 min food deprivation; the remaining birds were deprived for 120 min. Birds were weighed (to the nearest 0.1 g) before and after the food deprivation, change in body mass being the parameter of interest.

RESULTS

The effect of state on success (whether or not the mealworm was taken) was investigated with the McNemar's change test (Siegel and Castellan 1988) performed on SPSS (SPSS 1988). The distances reached from the perch, or distances travelled along the perch, number of attempts to obtain the mealworm and handling times were all compared by Wilcoxon's matched-pairs signed ranks test on MINITAB (Ryan et al. 1985). All tests were performed on paired data, from the same individual, from within-experimental trials. The results of all trials and associated P values (two-tailed tests are used throughout), are shown in Table 1. (There were only enough paired measures of handling time for comparison in trial 4.) There is a small but highly significant difference in the change in body mass between the two food deprivation treatments (Change in mass, 30 min deprivation, -0.50 ± 0.058 ; 120 min deprivation, -1.08 ± 0.133 ; Mann-Whitney test, $W = 21$, $P = 0.0043$; $n = 6$, in both groups).

In trials 1 and 2, the manipulation of energetic state significantly affected whether or not the mealworm was taken, with the high deprivation treatments taking the mealworm more often. The results also indicate that maximum distance reached, or travelled along the perch, may be affected similarly by the experimental manipulations. Although only significant in trial 1, the same "distance" trend is evident across all four trials. The observed difference in "success" is not simply a product of the high deprivation group making more attempts to obtain the food item, because the number

of attempts made by each group did not differ significantly in any of the trials. Increased deprivation time was also found to decrease handling time in trial 4. The apparent differences between trials may be attributable to any of a number of factors. It may be that the state-dependence of accessibility differs between tasks. Such a phenomenon could arise if different tasks have different levels of risk associated with them. Alternatively, although the foraging tests were designed to be near the reaching limits of the birds, this may not have been achieved to the same degree in all trials. Moreover, because I was predominantly interested in within-trial differences, brought about by changes in state, between-trial comparisons may be influenced by some undetermined longitudinal effect. However, any longitudinal effects, if present, will not influence the within-trial comparisons.

DISCUSSION

Although I was interested in the effects of energetic state on accessibility, it could be argued that the manipulations are confounded by changes in body mass, which itself could influence foraging ability (Lehikoinen 1986, Alerstam 1990, Witter and Cuthill, in press). A priori, this is extremely unlikely to influence the results of trials 1 and 3, where differences in mass, due to the number of mealworms eaten, amount to approximately 0.5 g (<1% of body mass). However, the effect of different deprivation times (trials 2 and 4) on body mass could have been larger and was, thus, investigated independently. In fact, differences in the changes in body mass, between the two treatments, were similarly small, amounting to 1%–1.5% of body mass. At present there is little reason to believe that these small changes in mass would result in detectable differences in locomotor performance or dexterity. The results, then, are consistent with the hypothesis that birds in a more highly deprived energetic state are more willing to perform risky (dangerous) foraging behaviors (such as reaching further from the perch) than birds which are less deprived. This seems to influence directly the apparent (measured) accessibility of food items.

These findings suggest that energetic state should be carefully controlled in studies of accessibility. For within-species analyses, administering fixed deprivation times may be sufficient. However, between-individual differences in fat storage, for example due to dominance (e.g., Baker and Fox 1978, Gosler 1987b, Piper and Wiley 1990), may mean that equal deprivation periods do not necessarily imply equal, between-individual, changes in energetic state. This problem will necessarily be enhanced in between-species comparisons. It may be possible to alleviate this difficulty, however, by administering long, pre-trial deprivation times, since, eventually, effects of state would be expected to reach an asymptotic value. At this point, measured accessibility would be related to limiting factors, such as morphology, which may be of interest to the study concerned. However, possible effects of very long deprivation times on changes in body mass in such manipulations should also be assessed.

Few previous studies of accessibility have been explicit in stating how, or if, energetic state has been

controlled, and this makes it difficult to determine whether or not confounding effects may have arisen. However, some potential difficulties with previous experimental designs seem apparent. Accessibility experiments which involved a number of tasks, performed successively or in the same trial (e.g., Partridge 1976a, Moermond and Denslow 1983), may have introduced confounding effects of satiation. Similarly, foraging trials of variable length (e.g., Moermond and Denslow 1983), or very lengthy trials, pose difficulties because of (variable) longitudinal changes in energetic state. The possible confounding effects of state are unlikely to have influenced the qualitative conclusions of these studies, however, because changes in motivation probably only influence accessibility markedly at, or near, the limits of the birds' reaching abilities. For this reason, studies which aim to quantify the limits of accessibility (e.g., Moermond and Denslow 1985, Moermond and Howe 1986) should pay particular attention to standardizing energetic state. This would be especially important where the between-species, or between-individual, differences are small (relative to the change in measured accessibility due to energetic state). Nevertheless, given that measures of accessibility are dependent upon both morphology and motivation, it would seem sensible for all subsequent studies concerned with measuring accessibility, to be more explicit in assessing, or controlling for, the effects of state.

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LITERATURE CITED

- ALERSTAM, T. 1990. Bird flight and optimal migration. *T.R.E.E.* 6:210–215.
- BAKER, M. C., AND S. F. FOX. 1978. Dominance, survival and enzyme polymorphism in Dark-eyed Juncos, *Junco hyemalis*. *Evolution* 32:697–711.
- BENKMAN, C. W., AND A. K. LINDHOLM. 1991. The advantages and evolution of a morphological novelty. *Nature* 349:519–520.
- CUTHILL, I. C., AND T. GUILFORD. 1990. Perceived risk and obstacle avoidance in flying birds. *Anim. Behav.* 40:188–190.
- CUTHILL, I. C., M. S. WITTER, AND L. CLARKE. 1992. The function of bill-wiping. *Anim. Behav.* 43:103–115.
- DENSLow, J. S., AND T. C. MOERMOND. 1982. The effect of accessibility on rates of fruit removal from neotropical shrubs: an experimental study. *Oecologia* 54:170–176.
- FEARE, C. 1984. *The starling*. Oxford Univ. Press, Oxford, England.
- GOSLER, A. G. 1987a. Pattern and process in the bill morphology of the Great Tit, *Parus major*. *Ibis* 129:451–476.
- GOSLER, A. G. 1987b. Aspects of bill morphology in relation to ecology in the Great Tit, *Parus major*. Ph.D.diss. Oxford Univ., Oxford, England.
- LEHIKIONEN, E. 1986. Winter ecology of passerines:

- significance of weight and size. Ph.D.diss., Univ. of Turku, Turku, Finland.
- LIMA, S. L. 1987. Vigilance while feeding and its relation to the risk of predation. *J. Theor. Biol.* 124:303–316.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619–640.
- MCNAMARA, J. M., AND A. I. HOUSTON. 1987. Starvation and predation as factors limiting population size. *Ecology* 68:1515–1519.
- MCNAMARA, J. M., AND A. I. HOUSTON. 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheor.* 38:37–61.
- MCNAMARA, J. M. 1990. The starvation–predation trade-off and some behavioural and ecological consequences, p. 39–59. *In* R. N. Hughes [ed.], *Behavioural mechanisms of food selection*, NATO ASI Series A, Life Sciences. Springer-Verlag, New York.
- MOERMOND, T. C., AND J. S. DENSLOW. 1983. Fruit choice in neotropical birds: effects of fruit type and accessibility on selectivity. *J. Anim. Ecol.* 52:407–420.
- MOERMOND, T. C., AND J. S. DENSLOW. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs* 36:865–897.
- MOERMOND, T. C., AND R. W. HOWE. 1986. Ecomorphology of feeding: behavioral abilities and ecological consequences, p. 2265–2270. *In* H. Ouellet [ed.], *Acta XIX Congressus Internationalis Ornithologici*, Vol. II, Univ. of Ottawa Press, Ottawa, Canada.
- NEWTON, I. 1967. The adaptive radiation and feeding ecology of some British finches. *Ibis* 109:33–98.
- PARTRIDGE, L. 1976a. Field and laboratory observations on the foraging and feeding techniques of Blue Tits and Coal Tits in relation to their habitats. *Anim. Behav.* 24:534–544.
- PARTRIDGE, L. 1976b. Some aspects of the morphology of Blue Tits (*Parus caeruleus*) and Coal Tits (*Parus ater*) in relation to their behaviour. *J. Zool. Lond.* 179:121–133.
- PIPER, W. H., AND R. H. WILEY. 1990. The relationship between social dominance, subcutaneous fat, and annual survival in wintering White-throated Sparrows (*Zonotrichia albicollis*). *Behav. Ecol. Sociobiol.* 26:201–208.
- PULLIAM, H. R., G. H. PYKE, AND T. CARACO. 1982. The scanning behaviour of Juncos: a game-theoretical approach. *J. Theor. Biol.* 95:89–103.
- RYAN, B. F., B. I. JOINER, AND T. A. RYAN. 1985. MINITAB handbook. 2nd ed. PWS-Kent, Boston, MA.
- SIEGEL, S., AND N. J. CASTALLAN. 1988. *Nonparametric statistics for the behavioural sciences*. 2nd ed. McGraw-Hill, Singapore.
- SNOW, B., AND D. SNOW. 1988. *Birds and berries*. Poyser, Calton, England.
- SPSS. 1988. *SPSSx user's guide*. 3rd ed. SPSS, Chicago.
- WITTER, M. S., AND CUTHILL, I. C. In Press. The ecological costs of avian fat storage. *Phil. Trans. Roy. Soc. B*.