

- CASH, K. J., & R. M. EVANS. 1986. Brood reduction in the American White Pelican (*Pelecanus erythrorhynchos*). *Behav. Ecol. Sociobiol.* 18: 413-418.
- DRENT, R. 1973. The natural history of incubation. Pp. 262-320 in *Breeding biology of birds* (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.
- EVANS, ROGER M. 1988a. Embryonic vocalizations and the removal of foot webs from piped eggs in the American White Pelican. *Condor* 90: 721-723.
- . 1988b. Embryonic vocalizations as care-soliciting signals, with particular reference to the American White Pelican. *Proc. Int. Ornithol. Congr.* 19: 1467-1475.
- . 1989. Egg temperatures and parental behavior during the transition from incubation to brooding in the American White Pelican. *Auk* 106: 26-33.
- . 1990. Effects of low incubation temperatures during the piped egg stage on hatchability and hatching times in Domestic Chickens and Ring-billed Gulls. *Can. J. Zool.* In press.
- , & K. J. CASH. 1985. Early spring flights of American White Pelicans: timing and functional role in attracting others to the breeding colony. *Condor* 87: 252-255.
- FORBES, M. R. L., & C. D. ANKNEY. 1988. Nest attendance by adult Pied-billed Grebes, *Podilymbus podiceps* (L.). *Can. J. Zool.* 66: 2019-2023.
- GRAVES, J., A. WHITEN, & P. HENZI. 1984. Why does the Herring Gull lay three eggs? *Anim. Behav.* 32: 798-805.
- GREENLAW, J. S., & R. F. MILLER. 1983. Calculating incubation periods of species that sometimes neglect their last eggs: the case of the Sora. *Wilson Bull.* 95: 459-461.
- GUILLION, G. W. 1954. The reproductive cycle of American Coots in California. *Auk* 71: 366-412.
- KNOPF, F. L. 1979. Spatial and temporal aspects of colonial nesting of White Pelicans. *Condor* 81: 353-363.
- . 1980. On the hatching interval of White Pelican eggs. *Proc. Okla. Acad. Sci.* 60: 26-28.
- LUNDY, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hen's egg. Pp. 143-176 in *The fertility and hatchability of the hen's egg* (T. C. Carter and B. M. Freeman, Eds.). Edinburgh, Oliver and Boyd.
- MOCK, D. W. 1984. Infanticide, siblicide, and avian nestling mortality. Pp. 3-30 in *Infanticide: comparative and evolutionary perspectives* (G. Hausfater and S. B. Hrdy, Eds.). New York, Aldine.
- MORTON, M. L., & M. E. PEREYRA. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). *Auk* 102: 25-37.
- NELSON, J. B. 1978. *The Sulidae, Gannets and Boobies*. Oxford, Oxford Univ. Press.
- NICE, M. M. 1954. Problems of incubation periods in North American birds. *Condor* 56: 173-197.
- SPELLERBERG, I. F. 1971. Breeding behaviour of the McCormick Skua *Catharacta maccormicki* in Antarctica. *Ardea* 59: 189-230.
- TSCHANZ, B. 1968. Trottelummen, Die Entstehung der persönlichen Beziehungen zwischen Jungvogel und Eltern. *Z. Tierpsychol. Beih.* 4: 5-100.
- WEBB, D. R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89: 874-898.

Received 11 September 1989, accepted 23 December 1989.

## Habitat Choice in Captive Arctic Warblers

KRISTEN C. VAN PATTEN AND TREVOR PRICE

Department of Biology, C-016, University of California-San Diego, La Jolla, California 92093 USA

Many closely related species of birds occupy distinct habitats, and reasons for such habitat choice are an active field of research (Cody 1985a). Still, there have been few studies on the development of habitat preferences in captive birds, and little assessment of the extent to which habitat choice is innate. Partridge (1974) simultaneously introduced several hand-reared individuals of two species of tits (*Parus*) into an aviary, and found that individuals of each species foraged in their naturally preferred habitat. Greenberg (1987) demonstrated that young Worm-eating Warblers (*Helmitheros vermivorus*) had innate preferences for foraging in a specific microhabitat (dead leaves), but

did not investigate broad-scale habitat choice. Several authors have shown that early experience can affect habitat preferences, although they did not always compare naturally available habitats (Klopfer 1963; Greenberg 1983, 1984; Gluck 1984).

Different species, and even subspecies, in the genus *Phylloscopus* (Old World leaf warblers) occupy distinct habitats (Gaston 1974, Cody 1985b, Price MS). For example, along an altitudinal gradient in Kashmir, India, some species are restricted to broad-leaved forest, some to coniferous forest, while others are more generalized (Price MS). In this study, we brought chicks of the Arctic Warbler, *Phylloscopus borealis*, into

captivity and investigated choice of coniferous and broad-leaved vegetation as foraging substrate. The Arctic Warbler breeds from Alaska to Finland and is divided into several subspecies (Williamson 1974). We studied the Alaskan subspecies, *P. b. kennicotti*, which breeds in willows (Price and Beck 1989) and winters in the tropical forests of southeast Asia (Williamson 1974). This subspecies is thus largely confined to broad-leaved trees, although coniferous trees may be encountered on migration. We wished to determine if broad-leaved trees were preferred over coniferous trees in simultaneous choice tests of naive birds, if any preferences could be modified as a result of short-term experience, and if any differences in habitat use were correlated with foraging efficiency.

In July 1988 we collected 10 Arctic Warbler chicks (aged 3–5 days) from three nests near Nome, Alaska (see Price and Beck 1989). We transported the chicks to San Diego and raised them on a diet of crickets, mealworms, meat, milk, and eggs. At the age of natural fledging, chicks were placed (in twos or singly) in small (60 × 40 × 40 cm) cages. Half the cages were supplied with a 0.5-m conifer branch (5 chicks) and half with a 0.5-m broad-leaved branch (5 chicks). Twenty days later, all chicks were separated into individual cages, without any natural foliage, and maintained on a diet of mealworms, wax moth larvae, and meat-egg mix. Our experiments began in January 1989 (when the birds were 6 months old) and continued until April 1989.

One bird was used to develop an appropriate procedure and was excluded from all analyses. The other nine birds were all subject to the same experimental protocol. Trials for each bird lasted seven days, and the birds were individually studied one after the other. The subject bird was placed in an indoor aviary (ca. 2 m<sup>3</sup>) in the afternoon of the day before the experiments began, and was kept continuously in the aviary for the seven days. We obtained four small potted trees (ca. 1-m high and 1-m across) from a local nursery: two specimens of *Ficus benjamina* (the broad-leaved representative) and two of *Pinus halepensis* (a short-needled conifer). Two trees were placed in the aviary at any one time. The two tree types were matched by height, however, they differed with respect to the total length of branches available for perching (see Klopfer 1963). The coniferous trees had 3–4-m total usable branch length, and the broad-leaved had 8–10-m total usable branch length.

A trial consisted of 30 min of detailed observation. Standard food was kept in the aviary in the early morning and evening. The food was removed from the aviary a minimum of 2 h before the first trial of the day, and apart from fruit flies (*Drosophila melanogaster*), the bird was not provided with any food until after the last trial of the day. Just before each trial, >300 fruit flies were shaken into each tree. We do not know if the flies remained in each tree to the same extent but, as we will show, birds foraged ac-

tively in each tree type and maintained similar capture rates. This suggests that many flies were present in both trees. During a trial, we recorded the time the bird spent in each tree, on the floor, and clinging to the sides of the aviary. We also recorded the number of feeding events in the two trees. We distinguished gleanings (when a bird picks from the vegetation without hopping or flying and which made up >93% of the total of 4,700 captures) from all other methods (e.g. flycatches, etc.). For each glean, we recorded whether head movements were up, down, or horizontal, and we recorded the substrate from which the fly was taken (leaf, branch, or trunk). Multiple pecks at the same position were recorded as a single feeding attempt. Most but not all attempts resulted in the capture of a fly. Because we were often unable to tell whether an attempt was successful or not, we simply tallied the total number of attempts.

On days 1 and 7, we placed one coniferous and one broad-leaved tree in the aviary. We conducted four trials on each day (two in the morning and two in the afternoon). On days 2 and 6 we also conducted four trials, but we alternated trials with both broad-leaved trees in the aviary with trials with both coniferous trees in the aviary. On days 3–5, we kept the two coniferous trees continuously in the aviary, and conducted two trials on day 3 and two trials on day 5. We kept the birds with only coniferous trees for three days to see if they would later come to prefer these trees when given a choice. We a priori expected the birds to show a preference for broad-leaved trees. Between all trials, we randomly rotated trees among positions in the aviary.

For statistical purposes we assumed that the performance of each individual bird was an independent data point, unless otherwise stated. Despite extensive observation, only very large differences will be significant at  $\alpha = 0.05$  because our sample size is nine. Each bird experienced one or other substrate type from 10 to 30 days of age, but not beyond. We found no obvious effect of this treatment on the different individuals' behavior. The four birds that experienced conifers at an early age actually spent slightly more time in broad-leaved branches than the five birds that experienced broad-leaved branches (expressed as a proportion of total time in the two tree types on days 1 and 7), but the differences were not significant (Mann-Whitney test,  $P > 0.1$ ).

On day 1, the nine birds averaged ( $\pm$ SE)  $43 \pm 12.5$  min in the broad-leaved tree and  $20 \pm 9.5$  min in the coniferous tree (data are summed over the four trials). The remainder of the time (57 min) was spent on the floor and sides of the aviary. On day 7, the birds averaged  $33 \pm 6.9$  min in the broad-leaved tree and  $16 \pm 5.2$  min in the coniferous tree. The time spent in the broad-leaved tree as a proportion of the total time in trees was 68% on day 1 and 67% on day 7. There is no evidence for any change in preference from day 1 to day 7. When the data from day 1 and

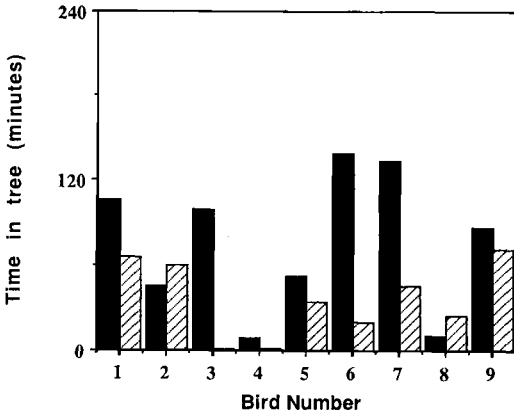


Fig. 1. Total time the nine individual warblers spent in the broad-leaved tree and the coniferous tree (summed over all trials on days 1 and 7). Note the extensive variability among individuals. Broad-leaved denoted by solid bar, coniferous by slashed bar.

day 7 are combined, there is a significant tendency for birds to forage more in the broad-leaved tree (Wilcoxon signed-rank test, two-tailed,  $n = 9$ ,  $P = 0.05$ ). During trials on days 2, 3, 5, and 6, the birds were not given a choice of habitat. They had to feed either in the tree type available or away from the trees altogether. When presented with no choice, the birds still spent less time in coniferous than in broad-leaved. In the coniferous-only trials, birds averaged  $9.6 \pm 1.0$  min in the trees ( $n = 4$  days). In the trials with only broad-leaved trees available, they averaged almost twice as long in the trees ( $17.5 \pm 2.8$  min,  $n = 2$  days). The difference is significant (two-tailed  $t$ -test, treating days as replicates,  $t = 3.5$ ,  $df = 4$ ,  $P < 0.05$ ).

These statistics mask considerable variation among individuals (e.g. Fig. 1). For example, on day 1, one individual spent no time in either tree, while another spent almost the whole time in the broad-leaved tree. However, there was consistency in where individuals were found in the morning and the afternoon on any one day. To test this statistically we calculated the proportion of variance among individuals using analysis of variance. Each individual defined a cell, with the time spent in a particular tree type in the morning and in the afternoon as the two measurements per individual. For all four comparisons (coniferous or broad-leaved on day 1 or day 7), there were significant differences among individuals ( $F$  tests, all  $P < 0.05$ ). Similar analyses that compared total times on day 1 with total times on day 7 were not significant ( $F$  tests,  $P > 0.1$  for broad-leaved,  $P > 0.5$  for coniferous), which suggests that individuals were not consistent across days.

During the first few days, birds foraged slowly and spent much time sitting in the trees. This is likely a reflection of the initial unfamiliarity with the envi-

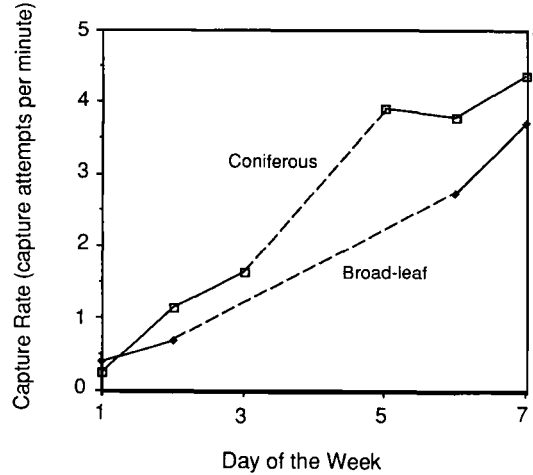


Fig. 2. Capture attempts on fruit flies (total capture attempts summed across all individuals/total time in each tree type) as a function of day after introduction of the bird to the aviary. There is a highly significant difference in the rate of capture attempts between days 1 + 2 and days 6 + 7 (Wilcoxon signed-rank test,  $n = 9$ ,  $P < 0.01$ ).

ronment. This was the first time that each individual encountered a tree or substantial space in which to move. Foraging rate rapidly increased (Fig. 2), and by day 5, birds foraged actively throughout the trials. We found no evidence for differences in the number of gleans as a proportion of all captures between broad-leaved and coniferous, or for differences in direction of head movements (Wilcoxon signed-rank tests, all  $P > 0.1$ ). However, birds tended to pick more from leaves versus other substrates in the coniferous (using data from days 6 and 7 only, 56% of all gleans from leaves) than the broad-leaved (50% of all gleans from leaves) (Wilcoxon signed-rank test, two-tailed,  $n = 7$  birds with complete data,  $P < 0.05$ ). Feeding attempts occurred at a slightly higher rate in the coniferous than the broad-leaved (Fig. 2), but differences were not significant (Wilcoxon signed-rank tests on days 6 and 7, both  $P > 0.1$ ).

In summary, birds tended to forage more in broad-leaved than coniferous trees. We do not know what cues were involved. One reason for the greater time spent in the broad-leaved trees may have been the greater length of branch available (Klopfer 1963), but there are many other differences between the two tree types. It would be ideal to make similar observations on individuals taken from a population that naturally occupies coniferous habitat, such as subspecies of the Arctic Warbler from Japan, *P. b. xanthodryas*, and determine the extent to which preferences differ. In the absence of such a control, we assume that the preference we observed was a direct response to vegetation type.

The preference for broad-leaved trees was not altered after three days of exposure to only conifers. Furthermore, foraging efficiency was similar in the two habitats, and preferences based on profitability differences should not develop. Such nonabsolute innate preferences for the naturally occupied habitat may be common (Greenberg 1987). They would result in the general use of the habitat to which the species is presumably best adapted coupled with the exploration of alternative habitats. Such alternative habitats, if they are not too different, may hold food sources which are sometimes exploited more efficiently. Habitat choice may only become more restricted in nature as a result of interspecific interactions (e.g. Reed 1982, Cody 1985a, b). Indeed Partridge (1974) found that each species showed much stronger preferences for their natural foraging substrate than we found in the single species investigated in this study.

We thank T. Langen, L. Liou, K. Marchetti, M. Pavelka, A. Richman, and D. Van Patten for help, advice, or both. We are very grateful to E. Gwinner and L. Liou for detailed advice on the raising of insectivorous birds.

#### LITERATURE CITED

- CODY, M. L. 1985a. An introduction to habitat selection in birds. Pp. 4-56 in *Habitat selection in birds* (M. L. Cody, Ed.). New York, Academic Press.
- . 1985b. Habitat selection in the Sylviane warblers of western Europe and north Africa. Pp. 86-129 in *Habitat selection in birds* (M. L. Cody, Ed.). New York, Academic Press.
- GASTON, A. J. 1974. Adaptation in the genus *Phylloscopus*. *Ibis* 116: 432-450.
- GLUCK, E. 1984. Habitat selection in birds and the role of early experience. *Z. Tierpsychol.* 66: 45-54.
- GREENBERG, R. 1983. The role of neophobia in determining foraging specialization in some migrant warblers. *Am. Nat.* 122: 444-453.
- . 1984. The role of neophobia in the foraging site selection of a tropical migrant bird: an experimental study. *Proc. Natl. Acad. Sci. (USA)* 81: 3778-3780.
- . 1987. Development of dead leaf foraging in a tropical migrant warbler. *Ecology* 68: 130-141.
- KLOFFER, P. H. 1963. Behavioral aspects of habitat selection: the role of early experience. *Wilson Bull.* 75: 15-22.
- PARTRIDGE, L. 1974. Habitat selection in titmice. *Nature* 247: 573-574.
- PRICE, T., & D. BECK. 1989. Observations on the breeding of the Arctic Warbler *Phylloscopus borealis* in Alaska. *Condor* 91: 219-221.
- REED, T. M. 1982. Interspecific territoriality in the Chaffinch and Great Tit on islands and the mainland of Scotland: playback and removal experiments. *Anim. Behav.* 30: 171-181.
- WILLIAMSON, K. 1974. Identification for ringers, 2: the genus *Phylloscopus*. Tring, British Trust for Ornithology.

Received 22 September, accepted 26 December 1989.