

mained nesting. However, productivity in 1995 was higher than in 1996 (D. G. Roseneau, pers. comm.), and 1996 may have been a more stressful year.

Murres are probably the deepest diving alcid (Piatt and Nettleship 1985), and alcids in general have higher wing loads than other flying seabirds (Pennycuik 1987). Either of these factors (i.e., pressure on a new incision due to diving, or increased wing load) may have affected bird behavior. Smaller transmitters would help in both regards.

Between species, nest abandonment was similar within the treatment group, but Common Murres were more likely to return to the colony after abandoning the nest. The number of Common Murres in the control group was too small for adequate statistical analysis, but it appears that both species were equally likely to return to the colony. Differences in the likelihood of abandoning the nest cannot be determined with this sample.

Other seabirds may be better adapted than murres, both physically and behaviorally, for implantation. Spectacled Eiders *Somateria fischeri* are larger than murres ($\geq 1,000$ g versus 896 ± 69 g) and remain inland several weeks after implantation, thus giving birds time to recuperate before the stresses of diving in a marine environment (Peterson et al. 1995). Harlequin Ducks (*Histrionicus histrionicus*) have been successfully implanted with VHF transmitters (D. Esler, pers. comm.), but the transmitters used are smaller and the depths the birds reach are probably much shallower. The effects of abdominal implantation may vary among species and also may depend upon transmitter design. Therefore, we suggest this method be assessed species-by-species. In the case of murres, we conclude that nesting behavior of implanted murres differs significantly from nesting behavior of nonimplanted murres. Data received after abdominal implantation must be interpreted with this in mind.

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CORRELATES OF CREEPING SPEED VARIABILITY IN TWO SPECIES OF TREECREEPERS¹

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Abstract. Foraging behavior of Short-toed Treecreeper *Certhia brachydactyla* and Eurasian Treecreeper *C. familiaris* was examined to test how well it fits a simple foraging model using data on arthropod distribution on tree trunks. Field observations in general

supported the model predictions. Short-toed Treecreeper crept, on average, slower than Eurasian Treecreeper. Both species crept more slowly on larger trees. Eurasian Treecreeper crept slower on thick English oaks than on thick Scotch pines. Both treecreepers moved slower when probing as compared to gleaning, which was expected as foraging technique strongly affects handling time.

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Key words: *Certhia brachydactyla*, *Certhia familiaris*, foraging behavior, optimal foraging hypotheses, treecreepers.

Treecreepers, *Certhia* spp., are useful subjects for modeling and testing optimal foraging hypotheses because of their simple foraging behavior. Treecreepers' foraging behavior on tree trunks consists of many repetitions of search-encounter-decide (Stephens and Krebs 1986). Treecreepers take prey of rather uniform size, especially in comparison to their body size (Kuitunen and Törmälä 1983, Kuitunen 1989, Suhonen and Kuitunen 1991). Therefore, we can assume that handling time for all prey is similar, depends mainly upon the foraging technique used, and is longer for probing than for gleaning (Osiejuk 1994, 1996).

If, following Holling (1959), T_s is the time spent searching and T_h is the time spent handling, then $T_s + T_h = T$, where T is all the time spent foraging on one tree. If we also assume that the speed of movements between encounters is constant, the mean speed of creeping should decrease with increasing prey density. Therefore, based upon these assumptions and data concerning food abundance on tree trunks, predictions about creeping speed on different tree species or trees with different diameter should be possible. However, most observational methods that have been used do not allow estimation of creeping speed on different tree species (Vanicsek 1985, Székely 1987, Suhonen and Kuitunen 1991). This paper presents predictions of a simple theoretical foraging model and compares them with creeping speed patterns in two treecreeper species.

METHODS

Field work was carried out during five winters between 1990 and 1995 in Wielkopolski National Park (52°15'N, 16°50'E), western Poland. The foraging behaviors of Short-toed Treecreeper *Certhia brachydactyla* and Eurasian Treecreeper *C. familiaris* were observed between 08:00 and 12:00, from 1 December to 28 February. To minimize the effect of weather, observations were made only on good days (temperature over -5°C, wind below 4° in Beaufort scale, no rain or snow). Observations, which were taken during walks in the study area, were not started where the birds were sighted but after their first flight among the trees. A maximum of three observations were made per individual before another bird was located. Amount of double and triple observations of the same individual was less than 2% of the data set in both species.

The following foraging variables were recorded and constituted any single observation: (1) tree species used for foraging (Scotch pine *Pinus sylvestris*, English oak *Quercus robur*, other), (2) tree diameter (cm) at breast height, (3) foraging technique (gleaning or probing), (4) height (m) of beginning and finishing of foraging on the tree (H_1 and H_2 , respectively), (5) movement patterns (straight or spiral), and (6) foraging time. More about observational methods and the study area can be found in Osiejuk (1994, 1996). Creeping speed ($m \text{ min}^{-1}$) was estimated as $S = (H_2 - H_1)/T$.

I analyzed only the observations of treecreepers for-

aging on oaks and pines where initial and final height of foraging were different. There were two reasons for this: (1) observations of birds foraging with no movement ($H_1 = H_2$) were often very short and may have been influenced by the observer and (2) sufficiently detailed data concerning arthropod abundance were available only for pine and oak. Observations were obtained for about 30 individual Eurasian Treecreepers and about 50 individual Short-toed Treecreepers each year. Abundance was estimated on the basis of regular mapping in 1991 and 1992 (Osiejuk 1993) and marking birds on the same study plot in 1996 and 1997 after this study was completed (Osiejuk and Kuczyński 1997, and unpubl. data). Consequently, pseudoreplication of observations was minimal.

I distinguished two patterns of movements along the trunk in treecreepers: straight and spiral (Osiejuk 1996). When the spiral pattern is observed, the real distance of movement is greater than obtained on the basis of $H_2 - H_1$. The percentage of spiral pattern use was similar in *C. brachydactyla* and *C. familiaris* (34% and 39%, respectively, $\chi^2_1 = 2.7$, $P > 0.09$).

Data on arthropod assemblage on the surface of tree trunks were taken from two earlier studies. Jackson (1979) showed that prey density and availability depend upon the structure of bark, which varies according to tree species and age. Therefore, one could expect that trees with greater diameter—that is, older, with more complicated bark surface—should be richer in arthropod supply than thinner trees of the same species. Dziabaszewski (1976) defined quantitatively and qualitatively how abundance of *Arachnoidea* changes in the course of the year on different tree species and on different parts of the tree. He also compared the abundance of *Arachnoidea* and *Insecta* giving complete and reliable data for testing the above mentioned model. Dziabaszewski (1976) confirmed that there is a significant difference in arthropod distribution on Scotch pines and English oaks. The overwinter abundance of arthropods on oaks depends mainly upon the initial number of spiders and insects on the whole tree. Each winter the majority of arthropods is forced to migrate from the tree canopy down to the trunk with numerous crevices in its bark, because dry leaves do not protect them from frost. In the case of pines, the extent of migration is much more dependent upon the weather because twigs with needles are a sufficient refuge during mild winters. Generally, arthropods were always more abundant on oaks than on pines. Dziabaszewski (1976) observed on average of 57 arthropods m^{-2} of Scotch pine bark and 186 m^{-2} of English oak bark.

MODEL AND PREDICTIONS

The model I consider is intended to be the simplest one possible that incorporates parameters of foraging place and foraging behavior and allows prediction of creeping speed pattern of treecreepers. I made the following predictions:

(1) Within the same tree species, creeping speed should be slower on trees with larger diameter as bark of thicker trees are more cracked and give more hiding places for arthropods (Jackson 1979).

(2) The creeping speed should be lower on oaks than

TABLE 1. Mean (\pm SD) creeping speed (m min^{-1}) in treecreepers with respect to tree species, tree diameter, and movement pattern.

Tree species	Tree diameter (cm)	Movement pattern	Short-toed Treecreeper	Eurasian Treecreeper
Pine	≤ 40	Straight	4.2 ± 2.9	4.0 ± 2.3
	> 40		3.3 ± 0.2	4.0 ± 2.1
Oak	≤ 40	Straight	4.3 ± 1.5	3.7 ± 2.6
	> 40		2.8 ± 1.6	4.1 ± 2.0
Pine	≤ 40	Spiral	2.3 ± 0.5	3.7 ± 0.2
	> 40		1.5 ± 0.1	3.8 ± 0.2
Oak	≤ 40	Spiral	2.6 ± 0.6	2.7 ± 0.9
	> 40		1.4 ± 0.1	1.3 ± 0.1

on pines because oak bark provides a richer arthropod supply.

(3) Creeping speed should be lower if probing is used, because this technique lengthens handling time in comparison to gleaning (Holling 1959, Stephens and Krebs 1986). *C. brachydactyla* probed less than half as often (about 4% of feeding time) as *C. familiaris* ($\chi^2_1 = 3.9$, $P < 0.05$). Therefore, differences in speed caused by gleaning:probing use ratio should be more apparent in *C. familiaris*.

RESULTS

A total of 560 observations was collected for *C. brachydactyla* and 420 for *C. familiaris*. Mean (\pm SD) duration of observations was 74 ± 98 sec for *C. brachydactyla* and 67 ± 70 sec for *C. familiaris*. Duration of observations did not differ between species ($t_{978} = 1.4$, $P > 0.1$). *C. brachydactyla* crept slower than *C. familiaris* (mean \pm SD = 2.95 ± 2.24 m min^{-1} and 3.61 ± 3.55 m min^{-1} , respectively; $t_{978} = -3.5$, $P < 0.001$). If only observations of foraging where $H_1 \neq H_2$ were considered, then creeping speed was 3.75 ± 1.84 m min^{-1} and 4.33 ± 3.46 m min^{-1} , respectively; $t_{789} = -3.0$, $P < 0.01$). The correlation between diameter of tree trunk and creeping speed was negative and significant for both species (*C. brachydactyla*, $r_s = -0.24$, $n = 442$, $P < 0.001$; *C. familiaris*, $r_s = -0.32$, $n = 351$, $P < 0.001$).

The comparisons of mean creeping speed in Table 1 suggest that there are factors, other than tree species, tree diameter, and movement pattern, for which observations differ from the model predictions. Short-toed Treecreeper crept distinctly faster on trees with smaller diameter, and in most cases such differences were significant (Table 1). In Eurasian Treecreeper the result was similar in only one case (Table 1). The differences between creeping speed on different tree species with similar diameter did not always confirm model predictions. There was no significant difference in creeping speed on pine and oak in Short-toed Treecreeper. Eurasian Treecreeper fits the model better as in most cases it crept slower on oak than on pine (Table 1).

Both treecreepers crept slower when used probing than gleaning, and in both cases the differences were significant (*C. brachydactyla* using gleaning 3.81 ± 1.85 m min^{-1} , using probing 2.07 ± 0.52 m min^{-1} ; $t_{425} = 4.0$, $P < 0.001$; *C. familiaris* using gleaning $4.11 \pm$

2.34 m min^{-1} , using probing 2.22 ± 1.25 m min^{-1} ; $t_{334} = 3.7$, $P < 0.001$). However, Short-toed Treecreeper used probing technique rarely; the difference in proportion of probing and gleaning used was significant ($\chi^2_1 = 3.9$, $P < 0.05$). This also is supported by the results of an ANCOVA with tree species, foraging technique, and movement pattern as factors and tree diameter as covariate. There was a significant movement pattern effect on creeping speed when controlling for the effect of tree diameter in Short-toed Treecreeper (ANCOVA; tree species, $F_{1,286} = 0.8$, $P > 0.4$; foraging technique, $F_{1,286} = 1.5$, $P > 0.1$; movement pattern, $F_{1,286} = 32.4$, $P < 0.001$; covariate tree diameter, $F_{1,286} = 15.8$, $P < 0.001$). In the case of Eurasian Treecreeper, there were significant effects of all factors on creeping speed when controlling for the effect of tree diameter (ANCOVA; tree species, $F_{1,237} = 29.3$, $P < 0.001$; foraging technique, $F_{1,237} = 41.6$, $P < 0.001$; movement pattern, $F_{1,237} = 31.2$, $P < 0.001$; covariate tree diameter, $F_{1,237} = 5.5$, $P < 0.05$).

DISCUSSION

The pattern of treecreepers' speed of movement in general supports the prediction of Holling's equation (1959). The crucial factor influencing creeping speed in this model is handling time, which is determined by foraging technique. In both species, the foraging technique used strongly affected creeping speed. Short-toed Treecreeper, however, used probing significantly less frequently than Eurasian Treecreeper. This difference and the significantly longer bills of Short-toed Treecreeper (bill length in the study area, *C. brachydactyla* = 15.4 ± 1.4 mm, *C. familiaris* = 13.1 ± 0.9 mm, $t_{14} = 3.9$, $P = 0.001$, Osiejuk and Kuczyński, unpubl. data) may be very important evolutionarily.

Among superficially dispersed prey that are equally available for both treecreepers, there are many prey hidden in crevices of different depth. One can easily imagine that in some cases Eurasian Treecreepers are forced to stop for a moment and use probing to catch an arthropod, whereas Short-toed Treecreeper can catch an arthropod by gleaning. Therefore, the Short-toed Treecreeper probably is better adapted to exploit deeper bark crevices, and this adaptation could be crucial in severe winters. Studies on the distribution of *Certhia* species/subspecies throughout Eurasia in regard to climate, forest type, and bill morphology would be valuable.

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INTERACTIONS BETWEEN BLACK-BILLED MAGPIE AND FALLOW DEER¹

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Abstract. Black-billed Magpies (*Pica pica*) were observed pecking on fallow deer (*Dama dama*) on 56 occasions. Ectoparasite removal was apparently the reason for this interaction. Birds preferred deer that were sitting to deer that were standing, and interacted preferentially with adult males over females or calves. Deer did not solicit cleaning and, on a few occasions, were observed to shake off birds. This interaction may be beneficial for magpies, because ectoparasites are a predictable source of food, but its effect on fallow deer remains to be investigated.

Key words: bird-ungulate interactions, Black-billed Magpie, fallow deer, *Pica pica*.

Several studies on large herbivore–bird interactions have described birds using ungulates as perches (Heat-

wole 1965), or removing their ectoparasites or fur (Isenhardt and DeSante 1985, Yosef and Yosef 1991, Fitzpatrick and Woolfenden 1996). The behavior of ungulates in response to birds landing on them ranges from adopting postures that facilitate parasite removal, to intolerant reactions. Black-tailed deer (*Odocoileus hemionus*) freeze when cleaned by Scrub-Jays (*Aphelocoma coerulescens*) (Isenhardt and DeSante 1985), whereas feral hogs and wild boar (both *Sus scrofa*) solicit cleaning by lying down when pecked by Common Crows (*Corvus brachyrhynchos*) and Black-billed Magpies (*Pica pica*) (Kilham 1982, Massei and Genov 1995). In contrast, oxpeckers sometimes induce horn-shaking by their hosts, possibly because oxpeckers prevent wound healing when removing ectoparasites (Watkins and Cassidy 1987).

Black-billed Magpies eat ticks from the back of elk (*Cervus canadensis*) (Linsdale 1946), but have not previously been described to interact with fallow deer (*Dama dama*). A significant number of opportunistic

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