Population Dynamics and Social Behavior of the Mistle Thrush Turdus viscivorus During Winter

Authors: Skórka, Piotr, and Wójcik, Joanna D.

Source: Acta Ornithologica, 40(1) : 35-42

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/068.040.0109

ACTA ORNITHOLOGICA
Vol. 40 (2005) No. 1

Population dynamics and social behavior of the Mistle Thrush *Turdus viscivorus* during winter

Piotr SKÓRKA[1*] & Joanna D. WÓJCIK[2]

[1]Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30–387 Kraków, POLAND, e-mail: skorasp@poczta.onet.pl
[2]Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 30–016 Kraków, POLAND, e-mail: wojcik@isez.pan.krakow.pl
[*]corresponding author

Skórka P., Wójcik J. D. 2005. Population dynamics and social behavior of the Mistle Thrush *Turdus viscivorus* during winter. Acta Ornithol. 40: 35–42.

Abstract. The density and behavior of the Mistle Thrush in Niepołomice Forest (southern Poland) and adjacent open areas were studied during winter (December–February) in 1996/97, 1998/99 and 2000/01. Mistle Thrush densities differed significantly from winter to winter, and the abundance of thrushes decreased as the season progressed. Bird density and mistletoe clump density were correlated positively. Birds held territories or congregated in flocks. The latter were sighted in the forest only during winter 1996/97, when the largest density of birds was noted. Flock size decreased progressively during that winter, but at the same time, the number of territorial birds remained stable. This suggests that by the end of the winter 1996/97 some birds from the flocks had begun to hold territories. Flocks were also seen in open areas, and displayed a preference for foraging on pastureland. Each individual territory in the forest consisted of several clumps of mistletoe on a few adjacent trees, which were defended against both conspecifics and other species such as *Pyrrhula pyrrhula*, *Turdus merula* and *Dendrocopos major*. The aggressive encounter rate was correlated positively with bird density but negatively with the progress of winter (the latter was correlated negatively with the berry supply). Surprisingly, it was not correlated with mistletoe clump density or temperature. During abundant berry years, the density of birds may have been so large that defending the fruit against numerous neighbors would have been energetically less profitable than communal foraging.

Key words: Mistle Thrush, *Turdus viscivorus*, aggressive behavior, flocking behavior, fruit defense, mistletoe, Niepołomice Forest

Received — Nov. 2004, accepted — May 2005

INTRODUCTION

Food source defense is very rare among fruit-eating birds during winter (Snow & Snow 1984, Wilson 1986). The best known examples are the Mistle Thrush, Fieldfare *Turdus pilaris* and Robin *Erithacus rubecula*, which form winter territories in places with abundant berries and defend them as long-term resources (Snow & Snow 1988, Cuadrado 1995). Birds defend resources against conspecifics as well as other species. Interestingly, territorialism can shift into flocking behavior (and *vice versa*), which was shown experimentally by Zahavi (1971) and Tye (1986).

Many factors influence a bird's decision to defend a fruiting plant: fruit caloric content, food abundance, its spatial distribution, presence of intruders and the bird body size (Tye 1986, Snow & Snow 1988). Food distributed in clumps make defense of the resources easier and profitable, especially against individuals of the same species (Zahavi 1971, Tye 1986, Matthysen 1990, Pomara et al. 2003). Additionally, individual energy gain for territorial birds should be higher than those feeding in flocks when intruders' pressure is negligible (Tye 1986). However, in case when food is more evenly distributed in space, defense of the resource might not be as profitable as foraging in flocks (Zahavi 1971).

The Mistle Thrush is the largest species of European thrushes (Cramp 1988, Snow & Snow 1988). Snow & Snow (1984, 1988) have studied its winter behavior in the United Kingdom. During this period, Mistle Thrushes feed mainly on fruits of various trees and shrubs and defend them as long-term food supply. The fruit defense is very efficient as result of the large body size of this thrush. Snow & Snow (1984) argue that the large body size of the species is an outcome of selective pressure favoring larger individuals able to defend food sources against other species more effectively.

In this paper, we present behavioral data for Mistle Thrushes wintering in forests and partly in fields of southern Poland. We investigated how food density affects number of birds and how territory defense depends on food density, temperature and density of competitors. Attention was also given to social strategies and their possible changes in time and space, as a consequence of food density and antagonistic interactions.

STUDY AREA

The Niepołomice Forest (50°01'–50°08'N, 20°13'–20°27'E) is situated in the western part of the Kotlina Sandomierska dale, about 20 km east of Kraków (southern Poland). The Niepołomice Forest area (108.5 km^2) is divided into two parts: northern (28 km^2), dominated by oak-hornbeam forest *Tilio-Carpinetum*, and southern (about 80 km^2), dominated by coniferous forest. Our study was carried out in the southern part where mixed oak-pine forest *Pino-Quercetum* predominates (Ćwikowa & Lesiński 1981, Gruszczyk 1981). Pines *Pinus sylvestris* are more common than oaks *Quercus* sp., spruces *Picea abies* and birches *Betula* sp. Clumps of Mistletoe *Viscum album* commonly occur on trees (mean 6.8 ± 5.3 clumps per tree ± SD, range: 1–32, n = 153 trees). The climate of the studied area is transitional from oceanic to continental (Suliński 1981). According to Wiszniewski (1973) mean yearly temperature is 8.2°C (in July: 18.5°C, in January: -3.0°C), annual rain-fall is 645 mm and mean snow cover thickness is 10 cm. The snow cover lies on average from the third week of December to the end of the second week of March. For a more de-tailed description of the study area, see also Wasilewski (1990) and Skórka & Wójcik (2003).

METHODS

Bird censuses

The data presented in our paper were gathered during three winter seasons: 1996/1997, 1998/1999 and 2000/2001. To calculate thrush density, we established two transects in a mature pine forest where birds were counted from the beginning of December to the end of February. Transect "A" (6 km) was surveyed during all winters and 8, 6, and 12 counts were made there respectively. Transect "B" (10 km) was established in 2000/2001 and 12 counts were made. We divided each transect into 1-km sections. All sections of the two transects were in the interior (at least 100 m from forest edge) of mature forest of similar type and only differed in number of mistletoe clumps. All birds seen or heard were counted in each section. To calculate bird density (individuals per 10 ha) we included all birds seen within a 50-m belt on each side of the transect assuming 100% detectability there (P. Skórka, unpubl.). However, in other analyses we used the density index — mean number of individuals per 1-km section, to enlarge sample size. Walking speed was about 2 km per hr during observations. Observations were done during good weather conditions (avoiding snowfalls, rain and wind). In December 2000, we counted all mistletoe clumps visible from ground level for every section of the transects. Then, we compared the number of mistletoe clumps per 1 km with mean thrush number per 1 km noted in each section. For this comparison we used mean bird density index only for December, because mistletoe bears fruits at the beginning of the winter (Stypiński 1997), and abundance of berries can be treated as constant for this month. Thus, the differences in thrush density in December among sections resulted probably only from the number of mistletoe clumps, rather than the number of berries.

To check if the birds in the sections with different densities of mistletoe stay the same long throughout winter we used the following index:

$$J = (n\, x_{mean})/(n_t\, x_{max})$$

where: n = number of effective censuses (where at least one bird was seen in the section), x_{mean} = mean number of birds noted in winter in the section, n_t = total number of censuses in the section, x_{max} = maximum number of birds seen in the section. We calculated this index for the 2000/2001 winter for all sections as it approximates how long birds stay in each section. If birds in a section were seen more frequently and in similar number, then the value of this index was higher. The maximum value of this index is 1, when the number of birds in a section was the same during all counts. We assumed that the count with the largest number o birds reflects the maximum number of territories in the section. This index also may indirectly indicate the habitat patches (sections) of better quality, if it is assumed that birds occur for a longer period in patches of better quality habitat.

Behavioral observations

Thrush behavior was observed during surveys, and we also carried out additional observations in other parts of the Niepołomice Forest. We noted behavior of every observed bird whenever possible (what it was eating, where it flew, etc.), and if birds seen on a transect were in flocks or territorial. In this study, a flock was defined as a group of at least three individuals keeping close to each other (on the same tree) and reacting in similar way (e.g., flying in one direction). Moreover birds in flocks always intensively foraged what was never observed in territorial birds which spent most of time guarding on the top of the tree with mistletoe.

All instances of fruit defense were noted. To determine how the rate of aggressive interactions in which one individual was involved, depended on mistletoe clump number and on the bird density index, we counted number of birds (as described above) and number of aggressive encounters in transect "A" on 23 December 2000 and in transect "B" on 22 December 2000. Every first bird seen in the section was selected for the observation of its aggressive behavior. We observed this individual thrush as long as possible, until we lost sight of it. Then, we selected the next bird met in the section and again observed it in the same way. Using a stopwatch, we noted all aggressive encounters involving one individual. Only observations of a bird for a period longer than 5 min were included in the analysis. We always tried to be sure that another observed bird was a different individual as we moved along the transect. In our opinion, this reduces the probability of meeting the same individual again, as birds were territorial. Finally, we compared rates of aggressive encounters per 5 min with bird density index (individuals per 1 km) and with the number of mistletoe clumps per 1 km. We pooled data for the two successive days of 22 and 23 December 2000 because of very similar weather conditions.

In 2000/2001 we also checked how the rate of aggressive interactions changed throughout the winter. In transect "A" we selected the section with the highest bird density (based on previous winters and initial observations in November) and we observed throughout the winter every single bird as previously described. The number of mistletoe clumps is constant, so other factors should influence bird behavior: bird abundance, berry supply and temperature. Thus, we compared rates of aggressive interactions in which a single bird was involved with the bird density index, season progression and the air temperature. Because mistletoe berry supply is very difficult to measure directly in the field, we used the progression of the season as an index of berry supply changes. We found that berry supply and progression of the season were negatively correlated ($r = -0.71$, $p = 0.009$) basing on following observations: we hang 11 clumps of mistletoe (received from the forest officer) on trees, low above the ground for easy access and visited them every 10 days from the beginning of December 2000. All berries were counted during the visits.

We also observed thrushes in an open area plot (about 350 ha) immediately adjacent to the Niepołomice Forest. This plot had 50% ploughland cover, 30% pastures and about 20% meadows with tall vegetation, as well as a few scattered shrubs and trees (including fruiting Hawthorn *Crataegus* sp. and Rowan *Sorbus aucuparia*).

In total, for the three winter seasons we made 58 surveys of all the study area (forest and farmland), which lasted together 359 hours.

Data analysis and statistics

For testing if bird density differed between winters, we used ANCOVA with date of census as a covariate. We used linear regression analysis to determine the relationship between mean index of density of birds in December 2000 within 1-km sections and mistletoe clump density index. We included in the model SD^{-1} as a weight because some equal means differed considerably in the variance. Means with smaller variance received higher weights. Spearman rank correlation was used to determine the relationship between index *J* and the index of mistletoe clump density.

For analyzing results from winter 1996/1997, we used Spearman rank correlation to test how flock size changed throughout the winter in the forest and to check if the number of territorial birds was stable.

To determine if the rate of aggressive encounters depended on bird density and density of mistletoe clumps (data from 22 and 23 December 2000), we divided the data according to bird density index into two easily distinctive groups: ≤ 5 and ≥ 6 individuals per 1 km and we used ANCOVA. To check how the rate of aggressive encounters changed with bird density, winter progression and temperature we used multiple regression analysis (data from one selected section).

We used chi-square statistics to verify if flocks in open areas preferred feeding on any type of determined habitats (plough-lands, pastures or meadows). To compare the average size of flocks in the forest and in open area we used a Mann-Whitney U-test.

Means are shown with ± SD. The level of significance was set at 0.05.

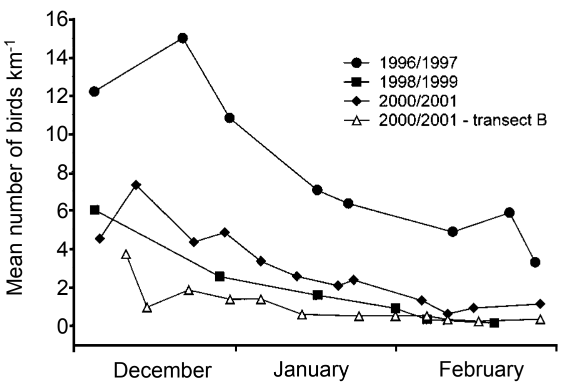

Fig. 1. Changes in Mistle Trushes number throughout winter.

RESULTS

Population dynamics

During 1996/1997, 1998/1999 and 2000/2001 the mean winter densities of Mistle Thrush were 5.6, 1.0 and 2.3 individuals per 10 ha, respectively. The number of birds decreased with winter progression (Fig. 1). Within transect "A" bird numbers differed between winters (ANCOVA $F_{2,22} = 49.5$, $p < 0.001$, Fig. 1). Mean bird density index in December was positively related to density index of mistletoe clumps ($R^2 = 0.68$, $F_{1,26} = 57.7$, $p < 0.001$, Fig. 2). Index *J* was positively correlated with number of mistletoe clumps per 1 km ($r_s = 0.77$, $p < 0.001$, Fig. 3).

Flocks of Mistle Thrushes in the forest were observed only in the winter of 1996/1997. We noted 23 flocks in the forest (mean flock size: 8.7 ± 5.6, range: 3–26 individuals). Flock size decreased throughout winter ($r_s = -0.81$, $n = 23$, $p < 0.001$). Surprisingly, the number of territorial birds was stable throughout the winter, and even at the end of the winter the number of territorial birds seemed to rise; however the difference was not significant ($r_s = 0.1$, $n = 8$ counts, $p = 0.823$, Fig. 4).

In open areas, we noted Mistle Thrushes exclusively in flocks during all winter seasons but only in warmer days with temperature over 0°C and reduced snow cover. We observed 13 flocks; nine were seen in pastures, two in plough-lands and two were seen in flight. It appeared that birds preferred feeding in pastures over other open areas ($\chi^2_2 = 14.3$, $p < 0.001$). The mean flock size in open areas was 5.4 ± 2.0 (range: 3–10) and differed from mean flock size in the forest (Mann-Whitney test, U = 75, p = 0.04). This difference remained significant even when only data for winter 1996–1997 were used (U = 23.5, p = 0.041).

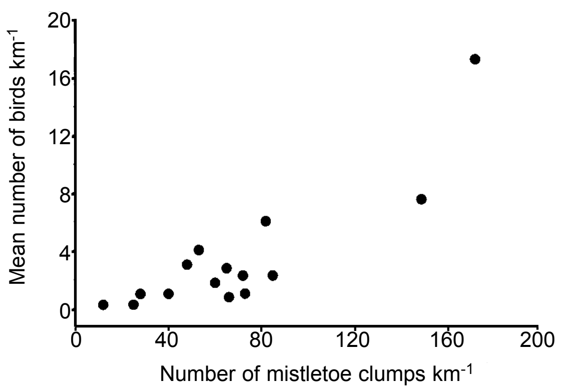

Fig. 2. Relationship between Mistle Thrush mean density index and density index of mistletoe clumps.

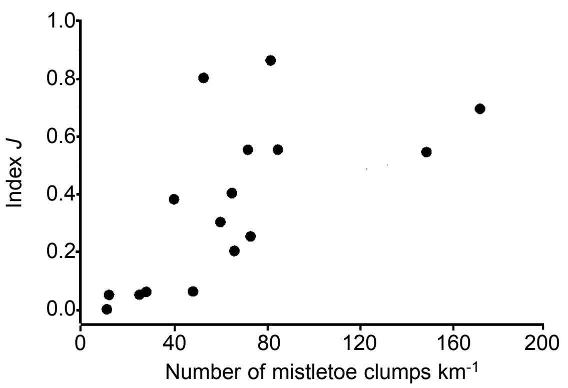

Fig. 3. Correlation between value of index *J* and density index of mistletoe clumps.

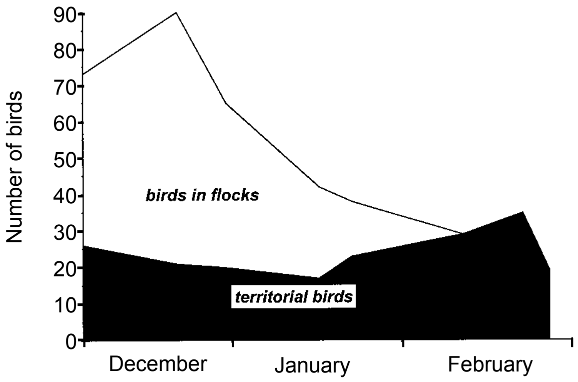

Fig. 4. Territorial Mistle Thrush number changes and observed in flocks throughout winter 1996/1997.

Diet

In the forest Mistle Thrushes were probably feeding almost exclusively on mistletoe berries (n = 240 observations), but in open areas they foraged on invertebrates, which were drawn out from the soil (mainly earthworms Lumbricidae, 29 of 34 observations). We did not see Mistle Thrushes feeding on fruits in open areas despite the occurrence of a few fruit shrubs there (mainly hawthorns;), probably because Fieldfare flocks foraged on the berries.

Territorial behavior

For twelve territories we managed to estimate exactly how many trees and mistletoe clumps on them are defended. The average territory defended by Mistle Thrushes in the Niepołomice Forest consisted of 3.3 ± 1.8 trees situated close together and 29.1 ± 6.7 mistletoe clumps on them. We did not found any significant correlation between number of tress defended by Mistle Thrush and number of mistletoe clumps on them ($r = 0.113$, $n = 12$, $p = 0.73$), what indicates that birds defended roughly constant number of mistletoe clumps. Every observed bird defended its territory alone and we have no evidence of territorial defense by bird pairs. We noted 422 aggressive encounters. Almost all of them were among Mistle Thrushes. We noted fruit defense against other species in only six cases: Bullfinch *Pyrrhula pyrrhula* (three cases), Blackbird *Turdus merula* (two cases), and Great Spotted Woodpecker *Dendrocopos major* (one case).

We found a significant effect of bird density on the aggressive encounter rate (ANCOVA $F_{1,18} = 6.9$, $n = 21$, $p = 0.017$), but surprisingly we did not find any effect of mistletoe density on the aggressive encounter rate (ANCOVA $F_{1,18} = 0.7$, $n = 21$, $p = 0.41$). The mean rate of aggressive encounters was 3.4 ± 2.7 per individual per 5 min (n = 61). The rate of aggressive encounters in which one individual was involved decreased with decreasing density index of thrushes and with winter progression (≈ berry supply); however it was not related to temperature (R^2 adjusted = 0.71, $F_{3,41} = 33.448$, $p < 0.0001$, n = 45, Table 1).

Table 1. Factors affecting aggressive encounter rate variation among Mistle Thrushes on one selected section (results of multiple regression analysis).

Variables	B	SE	t_{41}	p
Birds density	0.215	0.075	2.787	< 0.01
Winter progression	-0.049	-0.019	-2.520	< 0.02
Temperature	-0.079	-0.056	-1.415	< 0.2

DISCUSSION

Bird number, feeding behavior and flocks

Densities of Mistle Thrush differed between consecutive winters. Such fluctuations in number of individuals are characteristic for fruit-eating birds and depend mainly on food supply (Tyrväinen 1975, Simms 1978, Jordano 1993). In our study, the density index of Mistle Thrush was strictly related to the mistletoe clump density index. Mistle Thrush is known as a main seed vector for this plant species (Hardy 1969, Snow & Snow 1988, Vallauri 1998).

Observations of flocks during winter 1996/1997 indicate a high supply of mistletoe berries. Unfortunately, we do not have accurate quantitative data from our study area but in the Radłów-Wierzchosławice Forest (similar in area and forest habitats) situated about 40 km east of our study area, exceptionally abundant fruiting mistletoe berries were also noted during the winter 1996/1997 and a large number of Mistle Thrushes was observed (Walasz 2000). It is known that during seasons of high fruit supply large flocks of birds can sometimes be formed (Tyrväinen 1975, Jordano 1993). It seems that flock size in our study area did not differ from flocks of other areas (Cramp 1988, Jordano 1993).

We noted flocks in open areas at the Niepołomice Forest only during warm periods with no snow cover and they foraged mainly in pastures. This probably resulted from the fact that during warm weather the soil was soft enough to draw out invertebrates (Gerard 1967).

Additionally, low vegetation in pastures may be positively correlated with invertebrate abundance (Morris & Thompson 1998).

Territorial behavior

In our study area, birds held and defended territories that included a few trees with mistletoe clumps. Snow & Snow (1988) suggested that the large body size of Mistle Thrush is an outcome of selective pressure favoring larger birds that were able to chase away other species. In our study area, almost all aggressive interactions happened between conspecifics. It suggests that the intraspecific competition may be another mechanism responsible for large body size of Mistle Thrush.

Snow & Snow (1984, 1988) also suggested that tree characteristics and its location are important factors influencing fruit defense. In their opinion, trees should be rather tall and free-standing. Our study area was a vast forest, thus a different habitat than Snows' study area (farmland with hedges and gardens). In the Niepołomice Forest, trees grow close to each other and branches often touch, suggesting that they could be difficult to defend. However, fruit defense commonly occurred in our study area. Our results do not confirm Cramp's (1988) claim that dense forests are avoided by Mistle Thrushes. We therefore believe that tree characteristics and their location may have a second role in fruit defense. We further expect that the habitat structure plays a less important role in the occurrence of Mistle Thrush during winter, and that the dominant factor is food availability.

Fruit defense by Mistle Thrush was also observed in other parts of Poland (Walasz 2000) and in Ukraine (W. Bielański, pers. comm.). Compared to the United Kingdom, the aggressive interaction rate was surprisingly high (Snow & Snow 1984, 1988), but similarly decreased as winter progressed. It is probably correlated with a decrease of berry supply and therefore thrush density — causing the average bird to be involved in fewer conflicts (Cuadrado 1995). A higher aggressive encounter rate in sections with a larger number of birds probably indicates territorial overlap and/or their smaller size. A negative relationship between territory size and food availability is well known (Salomonson & Balda 1977, Myers et al. 1979, Enokson & Nilson 1983, Lott & Lott 1991, Johnson & Sherry 2001) and it was also found in this study. Simultaneously, within the sections with higher density of mistletoe clumps, birds were seen for longer time throughout the winter (Fig. 3). This suggests that despite a higher rate of aggressive interactions in sections with higher number of birds, profits from holding a territory in these places are higher than the costs spent on territory defense against many neighbors. Johnson & Sherry (2001) also demonstrated that birds show greater persistence in places with higher food abundance. Therefore, Mistle Thrush territories located in places with a lower number of mistletoes are probably of lower quality. These territories are larger, probably less effectively defended, and the defense is more costly.

Bird numbers decreased throughout winter. During the 1996/1997 winter, decrease of bird number was probably caused by reduction of flock size. During the remaining winters, Mistle Thrushes probably left the studied area. We did not observe that territory abandonment could be caused by flocks of other species or floaters of Mistle Thrushes, as described by Snow & Snow (1988), or by predators. The rate of fruit consumption is strictly negatively correlated with temperature (Snow & Snow 1984, Kwit et al. 2004). In Poland, winters are more severe than in United Kingdom, therefore we suppose that fruit intake rate in our study area was higher. Having in mind the high rate of aggressive encounters, it is possible that fruit depletion in our study area occurred faster. As a result, birds probably abandoned their territories earlier.

Territorialism versus flocking behavior

During the analysis of the Mistle Thrush abundance dynamic through the 1996/1997 winter season, the most surprising fact was that after excluding birds observed in flocks, the number of territorial birds did not drop, and even had slightly risen at the end of winter. Simultaneously, flock size decreased throughout winter. It suggests that some of individuals feeding in flocks started to feed alone and defend a territory. Similar shifts from flocking into territorialism were found by Zahavi (1971), who showed that White Wagtails *Motacilla alba* resorted to flock feeding when food was distributed evenly in the habitat and they defended food when it was aggregated in piles. Tye (1986) observed analogous changes in social behavior for Fieldfare. This species of thrush forms large flocks when food (berries) occurs in large supply (Tyrväinen 1975, Simms 1978). Moreover, Delestrade (1999) as well as Morris & Thompson (1998) showed that flock size might be positively correlated with food abundance. Therefore, when intrusion rate is high it might not be profitable to defend the territory. Such situation seems be possible when food abundance is high. As we showed the aggressive encounter rate is positively related to bird density thus when food supply is high the defense may not be more profitable as a result of many conflicts with neighbors or other intruders (see: Tye 1986, Stamps & Krishnan 2001).

ACKNOWLEDGEMENTS

We are grateful to François Génier and Michel Gosselin for reviewing English in the manuscript and their valuable suggestions. We also thank Michał Woyciechowski, Rafał Martyka, Robert Anderson, Piotr Tryjanowski and an anonymous referee for their critical comments. Student Naturalists' Club of Jagiellonian University partially financed this study.

REFERENCES

Cramp S. (ed.). 1988. The birds of the Western Palearctic. Vol. V. Oxford Univ. Press.

Cuadrado M. 1995. Territory characteristics and the attacks against intruders in migrant robins (*Erithacus rubecula*) wintering in the Mediterranean area. Ardeola 42: 161–166.

Ćwikowa A., Lesiński J. A. 1981. [Floristic differentiation of comunities of present forest vegetation of Niepołomice Forest]. Stud. Ośr. Dok. Fizjogr. 9: 159–196.

Delestrade A. 1999. Foraging strategy in a social bird, the Alpine Chough: effect of variation in quantity and distribution of food. Anim. Behav. 57: 229–305.

Enokson B., Nilson S. G. 1983. Territory size and population density in relation to food supply in the Nuthatch (*Sitta europaea*) (Aves). J. Anim. Ecol. 52: 927–935.

Gerard B. M. 1967. Factors affecting earthworms in pastures. J. Anim. Ecol. 36: 235–252.

Gruszczyk A. 1981. [Types of forest site of Niepołomice Forest]. Stud. Ośr. Dok. Fizjogr. 9: 205–219.

Hardy E. 1969. Mistle Thrushes and mistletoe berries. Bird Study 16: 191–192.

Johnson M. D., Sherry W. T. 2001. Effect of food availability on the distribution of migratory warblers among habitats in Jamaica. J. Anim. Ecol. 70: 546–560.

Jordano P. 1993. Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. Vegetatio 107/108: 85–104.

Kwit C., Levey D. J., Greenberg C. H., Pearson S. F., McCarty J. P., Sargent S. 2004. Cold temperature increases winter fruit removal rate of a bird-dispersed shrub. Oecologia 139: 30–34.

Lott D. F., Lott D. Y. 1991. Bronzy Sunbirds (*Nectarina kilimensis*) relax territoriality in response to internal changes. Ornis Scand. 22: 303–307.

Matthysen E. 1990. Nonbreeding social organization in *Parus*. Curr. Ornithol. 7: 209–249.

Morris L. P., Thompson F. R. III. 1998. Effect of habitat and invertebrate density on abundance and foraging behavior of Brown-headed Cowbirds. Auk 115: 376–385.

Myers J. P., Connors P. G., Pitelka F. A. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. Auk 96: 551–561.

Pomara L. Y., Cooper R. J., Petit L. J. 2003. Mixed-species flocking and foraging behavior of four Neotropical warblers in Panamanian shade coffee fields and forests. Auk 120: 1000–1012.

Salomonson M. G., Balda R. P. 1977. Winter territoriality of Townsend's Solitaires (*Myadestes townsendi*) in Pinion-Juniper-Ponderosa ecotone. Condor 79: 148–161.

Simms E. 1978. British Thrushes. Collins, London.

Skórka P., Wójcik J. D. 2003. Winter bird communities in a managed mixed oak-pine forest (Niepołomice Forest, southern Poland). Acta Zool. Cracov. 46: 29–41.

Snow B. K., Snow D. W. 1984. Long-term defense of fruit by Mistle Thrushes (*Turdus viscivorus*). Ibis 126: 339–349.

Snow B. K., Snow D. W. 1988. Birds and Berries. A study of an ecological interactions. T & AD Poyser, London.

Stamps J. A., Krishnan V. V. 2001. How territorial animals compete for divisible space: a learning-based model with unequal competitors. Am. Nat. 157: 154–169.

Stypiński P. T. 1997. [Biology and ecology of the mistletoe (*Viscum album*) in Poland]. Frag. Flor. Geobot. S. Pol. Suppl. 1.

Suliński J. 1981. [Outline of climate, relief and groundwater conditions in Niepołomice Forest]. Stud. Ośr. Dok. Fizjogr. 9: 55–98.

Tye A. 1986. Economics of experimentally-induced territorial defense in a gregarious bird, the Fieldfare (*Turdus pilaris*). Ornis Scand. 17: 151–164.

Tyrväinen H. 1975. The winter irruption of the Fieldfare (*Turdus pilaris*) and the supply of rowan-berries. Ornis Fennica 52: 23–31.

Vallauri D. 1998. Parasite dynamics of *Viscum album* L. in Austrian black pine stands in the Saignon watershed (southwestern Alps). Ann. Sci. Forest. 55: 823–835.

Walasz K. (ed.). 2000. The Atlas of wintering birds in Małopolska. Małopolska Ornithol. Soc., Kraków.

Wasilewski J. 1990. Dynamics of the abundance and consumption of birds of prey in the Niepołomice Forest. Acta Zool. Cracov. 33: 173–213.

Wilson M. 1986. Avian frugivory and seed dispersal in Eastern North America. Curr. Ornithol. 3: 223–280.

Wiszniewski W. 1973. [Atlas of the climate of Poland]. IMiGW, Warszawa.

Zahavi A. 1971. The social behaviour of the White Wagtail (*Motacilla alba*) wintering in Israel. Ibis 113: 203–211.

STRESZCZENIE

[Zagęszczenie i zachowania socjalne u paszkota w czasie zimy]

Paszkot w czasie zimy broni terytoriów lub występuje w stadach. Celem badań była próba określenia czynników wpływających na zmianę zachowań socjalnych tego gatunku. Badania prowadzono podczas trzech sezonów zimowych (1996/1997, 1998/1999 i 2000/2001) w Puszczy Niepołomickiej i przyległych terenach otwartych. Generalnie, liczebność ptaków malała z biegiem zimy (Fig. 1). Zagęszczenia paszkotów było dodatnio zależne od zagęszczenia kęp jemioły na drzewach (Fig. 2). W miejscach z większym zagęszczeniem kęp jemioły, ptaki pozostawały w

terytoriach dłużej niż w miejscach, gdzie zagęszczenie jemioły było mniejsze (Fig. 3). W Puszczy Niepołomickiej paszkoty najczęściej broniły terytoriów, złożonych z kilku lub kilkunastu kęp jemioły. Odnotowano także grupowanie się paszkotów w stada, które żerowały na jemiołach w Puszczy. Stada te obserwowano jedynie w czasie zimy 1996/1997, co zapewne miało związek z obfitym owocowaniem jemioły. Zaobserwowano, że w czasie tej zimy liczebność ptaków żerujących w stadach malała, zaś liczebność ptaków terytorialnych była stabilna ze słabą tendencją wzrostową (Fig. 4). Ponieważ podczas pozostałych zim liczebność ptaków terytorialnych także malała w ciągu sezonu (Fig. 1), wywnioskowano z tego, że ptaki ze stad zaczęły bronić terytoriów.

Paszkoty broniły terytoriów głównie przed innymi paszkotami, choć zaobserwowano także agresywne interakcje z innymi gatunkami: gilem, kosem oraz dzięciołem dużym. Liczba agresywnych zachowań w jednostce czasu, w które uwikłany był pojedynczy osobnik była pozytywnie skorelowana ze wskaźnikiem zagęszczenia ptaków i ujemnie związana z datą w sezonie (Tab. 1). Jednocześnie nie wykryto istotnego związku między liczbą agresywnych zachowań z zagęszczeniem kęp jemioły (Tab. 1). Uzyskanie wyniki sugerują, że w okresie dużej obfitości pokarmu, obrona terytorium jest nieopłacalna ze względu na duże zagęszczenie ptaków i wynikającą z tego dużą liczbę potencjalnych konfliktów.

Oprócz Puszczy Niepołomickiej, paszkoty obserwowano na przyległych do kompleksu leśnego terenach otwartych. Wszystkie ptaki przebywały w stadach. Dodatkowo odnotowano, że frekwencja spotkań stad paszkotów była statystycznie wyższa na pastwiskach niż na opuszczonych łąkach i polach uprawnych w stosunku do ich ogólnego udziału w powierzchni, co mogło się wiązać z łatwiejszym zdobywaniem pokarmu, który stanowiły bezkręgowce wyciągane z ziemi.