Ornis Fennica 84:32–38. 2007

Nest hole age decreases nest site attractiveness for the European Starling *Sturnus vulgaris*

Tomasz D. Mazgajski

Mazgajski, T.D., Museum and Institute of Zoology, Polish Academy of Sciences, 00-679 Warszawa, Poland. mazgaj@miiz.waw.pl

Received 17 March 2006, revised 4 August 2006, accepted 9 August 2006

I studied whether the European Starling *Sturnus vulgaris* has a preference for a particular age of their nesting hole in an old deciduous forest in Central Poland. I documented the probability that Starlings bred in natural holes (excavated by Great Spotted Woodpecker *Dendrocopos major*) of a known age in consecutive seasons. Occupation rates decreased linearly with a hole's age. Holes were occupied significantly more frequently in the first year after their excavation then older holes. Experimentally adding old nest material to nestboxes in order to simulate prior occupancy lowered the occupancy rate in a similar manner as observed in the natural cavities. Whereas avoidance of predation risk is the traditional explanation for avoidance of old sites, my results suggest that factors like presence of old nest material (with ectoparasites), and physical deterioration in the hole's quality should also be considered.

1. Introduction

Holes in trees are nest sites, which can be used by birds over many breeding seasons (e.g. Sedgwick 1997, Aitken *et al.* 2002, Kotaka & Matsuoka 2002). There are several studies describing species utilizing tree holes in relation to their characteristics (e.g. van Balen *et al.* 1982, Wesołowski 1989, Aitken *et al.* 2002, Bai *et al.* 2005). However, the temporal pattern of hole use is not well known (Sedgwick 1997, Kotaka & Matsuoka 2002). Due to the long lasting nature of these sites, birds nesting in tree holes in consecutive seasons are faced with at least two problems. First, predators are able to remember hole locations and penetrate them (e.g. Sonerud 1985). Hence, predation pressure increases in older cavities (e.g. Nilsson *et al.* 1991, Sorace *et al.* 2004). Thus, broods in older holes could be less safe and birds may prefer new nest sites unknown to predators (Sonerud 1985). On the other hand, secondary cavity nesters build nests for every breeding attempt. Nest materials may partially or totally decompose between seasons (Wesołowski 2000). But if the material does not fully decompose, it accumulates in the holes and this presents two additional problems for the birds. The increasing amount of nest material makes the site shallow. As a result, the distance between the active nest and entrance to the hole decreases, and the eggs/young are more vulnerable to predators (Wesołowski 2002). Second, ectoparasites, such as fleas and mites, can overwinter and develop in the old material (e.g. Rendel & Verbeek 1996), later infecting the host and its nestlings.

Due to both negative factors connected with the increasing age of tree cavity nest sites, one could assume a lower attractiveness and occupancy for cavity nesting birds, but only scant data exists that could confirm such a statement (Sonerud 1985, Korpimäki 1987, Kotaka & Matsuoka 2002). The relationship between nest site age and its usage has mostly been studied in relation to the impact of predation on birds' breeding success, and most often with the use of nest boxes (Sonerud 1985, Korpimäki 1987, Sorace *et al.* 2004). As for natural tree holes, this has not been verified as a factor except in the work of Nilsson et al. (1991).

The European Starling *Sturnus vulgaris* is a strongly competitive species in the group of secondary cavity nesters. It is able to usurp the cavities of many woodpeckers and other hole nesting species (e.g. Ingold 1989, Mazgajski 2000, Koenig 2003). Therefore, it could be assumed that the hole occupation rate of this species reflects its genuine preferences – including those related to the age of the holes – and not to existing options connected with the availability of empty holes in the breeding season. On the other hand, the Starling is one of the few species that is able to remove old nest material (Mazgajski *et al.* 2004). Therefore, a possible decrease in the attractiveness of a cavity due to age may not be observed in this species due to its nest site cleaning ability.

The nesting behaviour of the Starling has received much attention recently due to its strong competitive pressure on other hole-nesters, especially in North America (e.g. Ingold 1989, 1997, Mazgajski 2000, Koenig 2003, Wiebe 2003, Smith 2005). Some preferences in the general characteristics of usurped holes are described (Fisher & Wiebe 2006), and also knowledge of the Starling's preferences or lack of them in relation to a hole's age could be useful and may help to explain at least some cases of observed hole evictions. The Starling very frequently uses holes excavated previously by the Great Spotted Woodpecker *Dendrocopos major* (Wesołowski 1989). In general, woodpeckers excavate their own holes almost every year and utilize their old holes to a small degree. The eggs lie directly on the cavity bottom, thus their holes do not contain any nest material. In this way, they provide a resource for hole-nesters where the cavity age can be very easily and accurately established. Nest boxes that imitate natural holes also could be used for similar purposes (e.g. Sonerud 1985, Korpimäki 1987). However, they are designed to provide nesting birds with maximum protection from predators. Therefore, nest boxes could be especially useful in studying how old nest material and ectoparasite pressure influence hole utilization. Cleaned nest boxes imitate holes excavated by woodpeckers in previous seasons, and those containing old nests are similar to holes that had been used at least once by breeding Starlings.

The aims of this study were to establish whether old holes are less preferred by the Starling, as well as to analyze trends in woodpecker hole occupancy in relation to the age of the cavity and whether occupation in one year is related to utilization of the hole in the next breeding season by the species.

2. Study area

The study was carried out in the Bielański Forest reserve, ca. 145 ha. of old deciduous, mostly oak-hornbeam stands, located in the outskirts of Warsaw (Central Poland 52°N, 21°E). The number of tree holes – both natural and of woodpecker origin – is very high, so it could be assumed that no nest site limitations existed for hole-nesting birds. It was estimated that ca. 16 Great Spotted Woodpecker pairs and 250–300 Starling pairs breed there (Mazgajski *et al.* 2001). Woodpeckers excavate their holes relatively high above the ground – more than 65% of Great Spotted Woodpeckers' nests were above 10 m. (more information about woodpecker nests in Mazgajski 1998). Predators able to penetrate woodpecker holes include the Pine Marten *Martes martes*, Red Squirrel *Sciurus vulgaris* and Weasel *Mustela nivalis*.

An additional experiment with nest boxes was carried out in 103 ha. of old, mixed and deciduous forest located about 3 km. north of the main study area. Tree holes in this forest were also very abundant, similar to the Bielański Forest.

3. Methods

3.1. Natural nest sites

The study was carried out in 1992–1997. Only holes excavated by the Great Spotted Woodpecker were used for the analysis. I found almost all Great Spotted Woodpecker nests in the study area every year, mostly by listening for the begging calls of

Table 1. Number of holes occupied by the Starling in studied breeding seasons in relation to holes' age. Number of available holes in each age class is in parentheses.

	Age of the holes				
Season	t + 1	t + 2	t + 3	t +4	t + 5
1993	7 (13)				
1994	11 (12)	6 (13)			
1995	8 (10)	7 (10)	5 (12)		
1996	11 (13)	6 (10)	5 (10)	3 (11)	
1997	3 (5)	6 (12)	4 (9)	4 (10)	3 (11)

the young. Reuse of old holes by this species in the study area was very rare (only two cases out of 64 broods found). Therefore, the exact age of the holes was known and described as: t – for the year of hole excavation (active woodpecker nest), t + 1 – the next breeding season after the hole excavation, etc. Nest trees were marked and a sketch of the nest entrance location was drawn to ensure that the occupancy of the appropriate hole could be described in following seasons. These holes were checked for the presence of breeding Starlings in successive seasons. As the holes were generally high above the ground and thus inaccessible, only data about occupation rates were collected. The holes were observed (mostly in the second half of May) from the ground for up to 10 minutes, because this is enough time to detect breeding Starlings (Gromadzki 1978). Whitewash of faeces below the hole entrance also indicates occupancy by Starlings. Whenever there was no sign of hole occupancy, controls were repeated once more later in the season. Holes that seemed unusable (the tree or its fragment with the hole had fallen or was cut, the cavity entrance decreased due to injury compartmentalization, etc., cf. Wesołowski 2001) were excluded from the analysis.

To establish if Starling occupation in a given year is related to utilization of the hole by the species in the next breeding season, all data where information was gathered for the following season were used (n = 108 two year series from 49 holes).

3.2. Artificial nest sites

In order to establish Starlings' reaction to nest sites that either contained or were devoid of old nests, experiments with nest boxes were carried out in 1997 (as part of a larger project – see Mazgajski 2003 and Mazgajski *et al*. 2004 for details). The dimensions of the nest boxes (especially the depth (22 cm) and entrance diameter of 4.8–5 cm) were similar to Great Spotted Woodpecker holes (cf. Sandstrom 1992). Nest boxes without old nests (n = 24) imitated holes excavated by woodpeckers in the previous season (t + 1), and those that contained nest material (n = 28) were similar to those used by secondary cavity nesters for at least one season (≥ t + 2). Boxes with at least one egg laid were counted as occupied.

The relation between the occupation rate (in%) in particular breeding seasons and the hole's age were analyzed using the linear regression, and the proportions of holes used in distinctive classes were compared with the two tailed Fisher exact test. All analyses were performed using Statistica 4.3 software.

4. Results

4.1. Next year's occupancy

The status of the nest hole (occupied or not) in the first year strongly affected the status in the next season (Fisher exact test, $p < 0.003$). Among the 67 holes occupied by Starlings in a given year, about 57% were also used in the next year, whereas 27% (n = 41) of holes not used in a given year were occupied in the following season. Of holes not used in a given year, 73% of were also not used in the next season.

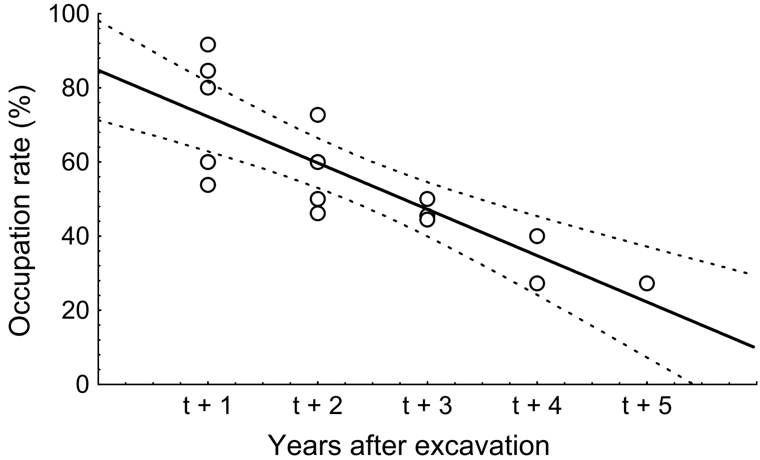

Fig. 1. Starlings' occupation rate in relation to the age of the nest holes (linear regression and its 95% confidence intervals). Each point for age classes represents data gathered in different breeding seasons.

4.2. Occupancy over time

During the study, 62 woodpecker nests were found. Some of them became unusable in the course of the study, therefore 11 holes were followed for a full five years after excavation (t + 5), 21 for four year (t + 4), 31 for three years (t + 3), 46 for two years (t + 2), and 53 were observed in the first year after excavation (t + 1). During successive seasons, occupation rates in particular hole age classes were similar (χ^2 test all cases P > 0.05) (Table 1).

In general, holes in the first year after excavation (t + 1) were occupied to a high degree (76%, n = 53), and almost significantly more frequently (57%, n = 45) than in the second year after excavation (t + 2)(Fisher exact test, P = 0.056). Older holes were occupied significantly less frequently than t + 1 holes (Fisher exact test, P < 0.01, all cases), but holes older than t + 1 (e.g. t + 2 and older) were utilized similarly (Fisher exact test, p < 0.1) (Table 1).

Occupation rates decrease with the holes' age ($y = 84.73–12.5x$, $F_{1,13} = 28.65$, $P < 0.0002$) (Fig. 1). Using the regression equation, it could be estimated that holes excavated seven years ago (t + 7) or more would not be used for breeding by the Starling.

4.3. Artificial nests

Nest boxes without old nests, which imitated t + 1 holes, were slightly preferred over those containing old nests (occupation rate 71%, n = 24 and 46%, n = 28 respectively, Fisher exact test p = 0.096). Data from holes were fully comparable with those from nestboxes (t + 1 holes and empty boxes – Fisher exact test, P = 0.78; t + 2 holes and boxes contained old nests, Fisher exact test, P = 0.47).

5. Discussion

As holes become older, their attractiveness to cavity nesting birds decreases, especially for the Starling, which is able to drive away other hole nesters and occupy the best holes. The results of some studies indicate that only a small portion of available holes are utilized by cavity nesters (e.g. Sandstrom 1992, Wesołowski 2001). This suggests that in many areas nest site limitation is not a factor for this group of birds as was previously thought (Newton 1994), but also that birds can choose the most suitable cavities, with the age of the holes being one possible criteria of nest site choice.

For Starling as well as for other cavity nesters there are at least two negative factors connected with the increasing age of holes considered thus far – predator pressure and ectoparasites.

The pattern of hole occupation observed in this study referred mainly to pairs that successfully raised their young. Therefore, it is possible that such results confirm the statement about the increasing pressure of experienced predators as holes become older (Sonerud 1985, Nilsson *et al.*

1991, Sorace *et al.* 2004). However, most of those studies were based on holes of the Black Woodpecker *Dryocopus martius* or on nest boxes with large entrances similar to such holes. Some of those studies indicate that breeding success is lower in old nest sites (Sonerud 1985, Nilsson *et al.* 1991), while others did not confirm this (Korpimäki 1987, Lang & Roost 1990). In general, the size of the entrance influences the rate of predation (Sandstrom 1992). Therefore, holes of medium-sized woodpeckers could be safer. The nesting success of Starlings breeding in holes is very high and observed nest predation concerned mostly pairs which bred in relatively low sites, below 4 m. (Nilsson 1984). Thus, in the study area where most Starlings bred above 10 m (own data), predation was probably rather weak. Therefore, the observed pattern of hole occupancy probably is not strongly affected by predation pressure, and reflects the birds' actual preferences. Korpimäki (1987) observed a similar trend in nest box choice relative to its age, and predation was very low in his study.

Predator pressure connected with shallower nest sites due to accumulated nest material is also probably not a problem for breeding Starlings due to its nest site cleaning ability. It was found that old nest material is removed to a larger extent in shallow nest sites than in deeper sites (Mazgajski *et al.* 2004). In this way, the Starling itself controls the distance between the entrance and eggs and nestlings.

The other factor that could explain the observed pattern of nest site occupancy is the presence of old nest material, and connected with this, the birds' investment in nest site cleaning as well as the pressure of ectoparasites. Fleas overwinter, emerge and leave old nests, to wait for hosts near the hole entrance at the beginning of the breeding season. Hole nesters may recognize such a congregation of fleas and avoid such nest sites (de Feu 1982). Therefore, the low occupancy of old holes may reveal the ability to avoid ectoparasites and parasitized nest sites (e.g. Oppliger *et al.* 1995). Starlings usually do not remove all of the old nest material if the site is deep enough (Mazgajski *et al.* 2004). The dried leaves and grasses used by Starlings in nests do not totally decompose (Wesołowski 2000), thus leading to higher ectoparasite loads in nests built on old nest material in comparison with cleaned nest sites observed in this species (Mazgajski & Kędra – unpubl. data). Therefore, it seems that the accumulation of nest material and possibly also the impact of ectoparasites shape the occupation rates of holes of different ages. This is supported by an almost identical nest box occupation rate with and without old nests, and holes t + 1 and older.

Based on experiments with nest boxes, Starlings prefer deeper nest sites without old nests (Mazgajski 2003). Therefore, it could be expected that this species would prefer holes without old nests – excavated by woodpeckers in the previous year (t + 1) to minimize the investment in nest site preparation. The results obtained confirm such a hypothesis. Preferences for such nest sites can also explain some cases of eviction from freshly excavated holes even when other artificial nest sites were abundantly available (Ingold 1997).

Another factor, which is relatively poorly studied and generally not considered in relation to hole age and its utilization by cavity nesters are changes in the physical properties of the entire tree and the hole itself over the years. With age, the walls of holes may soften and lose their thermoinsulation properties (Hooge *et al.* 1999, Wiebe 2001). Holes may get wet from rain and their internal dimensions may also change. All these factors may influence holes' microclimate conditions. As the microclimate may affects birds' reproduction (e.g. Wiebe 2001), this may also be a consideration in nest site selection (e.g. Wachob 1996). Physical deterioration is another factor that should be taken into consideration in addition to predators, old nest material and ectoparasites in studies of nest site age in cavity nesters. Certainly all these factors may work synergistically. At this time, it is difficult to establish which of them is most responsible for the results obtained, especially given that some additional information, such as breeding success, nestling condition and microclimate conditions in relation to the age of the holes were not collected in this study.

Hole nesters breeding in natural cavities have recently received much attention (Carlson *et al.* 1998, Aitken *et al.* 2002, Bai *et al.* 2003, Martin *et al.* 2004, Bai *et al.* 2005, Remm *et al.* 2006). But in analyzing the data, one should bear in mind that the age of a hole could also be considered as a factor affecting the results obtained. The decrease of a hole's attractiveness may not always be related to predators' behavior, but also to it being filled with nest material and the possible impact of ectoparasites, or to some type of physical deterioration in the hole's quality. In the case of the Starling, investments related to nest preparation could also be considered.

Acknowledgements. I would like to thank Aleksander Kędra for field assistance in nest box study and Jerzy Mazgajski for all logistic support. Barbara Przybylska reviewed the English version of this paper. This study was supported by the Polish State Committee for Scientific Research (KBN) grant no. PBZ-KBN-087/P04/2003.

Kottaraiset suosivat uusia pesäkoloja vanhojen kustannuksella

Keski-Puolassa tutkittiin, suosivatko kottaraiset tietyn ikäisiä pesäkoloja. Tutkimuksessa käytettiin käpytikan tekemiä koloja, joiden ikä tunnettiin. Pesimätodennäköisyys koloilla laski tasaisesti kolojen iän myötä. Edellisvuoteiset käpytikan kolot olivat merkitsevästi suositumpia kuin tätä vanhemmat. Vanhojen pesäpohjien laittaminen kottaraisille tehtyihin pönttöihin vaikutti myös negatiivisesti pesimätodennäköisyyteen. Tulokseni viittaavatkin siihen, että vahojen pesien predaatioriskin lisäksi niiden kunnon heikkeneminen sekä mahdollisesti suurempi loismäärä saattavat vaikuttaa kottaraisilla pesäpaikan valintaan.

References

Aitken, K.E.H., Wiebe, K.L. & Martin, K. 2002: Nest-site reuse patterns for a cavity nesting bird community in interior British Columbia. — Auk 119: 391–402.

Bai, M.-L., Wichman, F. & Mühlenberg, M. 2003: The abundance of tree holes and their utilization by hole-nesting birds in primeval boreal forest of Mongolia. — Acta Ornithologica 38: 95–102.

Bai, M.-L., Wichman, F. & Mühlenberg, M. 2005: Nest-site characteristics of hole-nesting birds in a primeval boreal forest of Mongolia. — Acta Ornithologica 40: 1–14.

Carlson, A., Sandström, U. & Olsson, K. 1998: Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. — Ardea 86: 109–119.

du Feu, C.R. 1982. How tits avoid flea infestation at nest sites. — Ringing & Migration 13: 120–121.

Fischer, R.J. & Wiebe, K.L. 2006: Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. — Oecologia 147: 744–753.

Gromadzki, M. 1978: Abundance of starling, Sturnus vulgaris L., in the breeding season in the vicinity of Gdańsk. — Acta Ornithologica 16: 325–334.

Hooge, P.N., Stanback, M.T. & Koenig, W.D. 1999: Nest-site selection in the Acorn Woodpecker. — Auk 116: 45–54.

Ingold, D.J. 1989: Nesting phenology and competition for nest sites among Red-headed and Red-bellied woodpeckers and European Starling. — Auk 106: 209–217.

Ingold, D.J. 1997: Do nest boxes help alleviate nest-site competition by European Starling on Northern Flickers? — Sialia 19: 83–91.

Koenig, W.D. 2003: European Starlings and their effect on native cavity-nesting bird. — Conservation Biology 17: 1134–1140.

Korpimäki, E. 1987: Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's Owl Aegolius funereus. — Journal of Animal Ecology 56: 185–196.

Kotaka, N. & Matsuoka, S. 2002: Secondary users of Great Spotted Woodpecker (Dendrocopos major) nest cavities in urban and suburban forest in Sapporo City, northern Japan. — Ornithological Science 1: 117–122.

Lang, E. & Rost, R. 1990: Brutaktivität, Bruterfolg und Schutz des Schwarzspechtes Dryocopus martius. — Vogelwelt 111: 28–39.

Martin, K., Aitken, K.H. & Wiebe, K.L. 2004: Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. — Condor 106: 5–19.

Mazgajski, T.D. 1998: Nest-site characteristic of Great Spotted Woodpecker Dendrocopos major in Central Poland. — Polish Journal of Ecology 46: 33–41.

Mazgajski, T.D. 2000: Competition for nest sites between the Starling and other cavity nesters – study in forest park. — Acta Ornithologica 35: 103–107.

Mazgajski, T.D. 2003: Nest site choice in relation to the presence of old nests and cavity depth in the Starling Sturnus vulgaris. — Ethology, Ecology and Evolution 15: 273–281.

Mazgajski, T. D., Kêdra, A. H. & Beal, K. G. 2004: The pattern of nest- site cleaning by European Starling Sturnus vulgaris. — Ibis 146: 175–177.

Mazgajski, T.D., Rejt Ł., Chromy M. & Podlacha F. 2001: Present status and changes in avifauna composition in "Bielański Forest" reserve. — Parki Narodowe i Rezerwaty Przyrody 20: 27–41. (In Polish with English summary).

Newton, I. 1994: The role of nest-sites in limiting the numbers of hole-nesting birds: a review. — Biological Conservation 70: 265–276.

Nilsson, S.G., Johnsson, K. & Tjernberg, M. 1991: Is avoidance by black woodpeckers of old nest holes due to predators? — Animal Behaviour 8: 439–441.

Oppliger, A., Richner, H. & Christe, P. 1994: Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (Parus major). — Behavioural Ecology 5: 130–134.

Remm, J., Lõhmus, A. & Remm, K. 2006: Tree cavities in riverine forests: What determines their occurrence and use by hole-nesting passerines? — Forest Ecology and Management 221: 267–277.

Rendell, W.B. & Verbeek, N.A. 1996: Are avian ectoparasites more numerous in nest boxes with old nest material? — Canadian Journal of Zoology 74: 1819–1825.

Sandstrom, U. 1992: Cavities in trees: Their occurrence, formation and importance for hole-nesting birds in relation to silvicultural practise. — Uppsala: SLU Rapport 23.

Sedgwick, J.A. 1997: Sequential cavity use in a cottonwood bottomland. — Condor 99: 880–887.

Smith, K.W. 2005: Has the reduction in nest-site competition from Starling Sturnus vulgaris been a factor in the recent increase of Great Spotted Woodpecker Dendrocopos major numbers in Britain? — Bird Study 52: 307–313.

Sonerud, G.A. 1985: Nest hole shift in Tengmalm's Owl Aegolius funereus as defence against nest predation involving long-term memory in the predator. — Journal of Animal Ecology 54: 179–192.

Sorace, A., Petrassi, F. & Consiglio, C. 2004: Long distance relocation of nestboxes reduces nest predation by Pine Marten Martes martes. — Bird Study 51: 119–124.

van Balen, J.H., Booy, C.J.H., van Franeker, J.A. & Osieck, E.R. 1982: Studies on hole-nesting birds in natural nest-sites. 1. Availability and occupation of natural nest-sites. — Ardea 70: 1–24.

Wachob, D.G. 1996: A microclimate analysis of nest-site selection by Mountain Chickadees. — Journal of Field Ornithology 67: 525–533.

Wesołowski, T. 2000: What happens to old nests in natural cavities? — Auk 117: 498–500.

Wesołowski, T. 2001: Ground check – an efficient and reliable method to monitor holes' fate. — Ornis Fennica 78: 193–197.

Wesołowski, T. 2002: Anti-predator adaptations in nesting Marsh Tits Parus palustris: the role of nest-site security. — Ibis 144: 593–601.

Wiebe, K.L. 2001: Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? — Auk 118: 412–421.

Wiebe, K.L. 2003: Delayed timing as a strategy to avoid nest-site competition: testing a model using data from starlings and flickers. — Oikos 100: 291–298.