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Food caching in the European Nuthatch *Sitta europaea*

HANS KÄLLANDER

Abstract

The behaviour and cache sites of European Nuthatches storing naturally occurring beech *Fagus sylvatica* and hazel *Corylus avellana* nuts in a South Swedish wood are described. Data are also given on the retrieval of cached nuts in winter and on recaching. On average it took a Nuthatch about 1 min to cache a beech nut. A third of all caches were below 1 m, 20% in the ground. Of those in trees, most were at heights between 5 and 15 m and less than 20% on branches thinner than 4 cm; of caches made above ground, 43% were in dead, often rotten wood. The choice of cache site was related to the kind of item to be cached: a higher proportion of hazel than beech nuts was cached in the ground. Oak was used proportionally more, and other species of tree proportionally less for caching than suggested by their abundance, perhaps because oak presented much dead wood which was extensively used for caching. More than 80% of all caches were covered with material from the immediate surroundings of the cache site. The Nuthatches removed the seed coat from a high proportion of the beech nuts before caching them; however, none of those cached in the ground and similar sites were shelled. During the coldest part of the winter, 1.1 nut per hour was retrieved in a winter following a poor mast crop vs 4.6 in a winter following a rich one. Recaching was common at all times but less so in winter.

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Introduction

Nuthatches (Sittidae) are among those avian taxa in which food storing is most wide-spread (Löhrl 1988), suggesting that the behaviour evolved early in the evolutionary history of this family.

For the European Nuthatch *Sitta europaea* there exists an early published record of food storing. Thus, already about a century ago the Swedish geologist and naturalist A.G. Nathorst described this behaviour in a paper entitled "The Nuthatch's planting of cereal grains in the trees" (Nathorst 1897; author's translation of the Swedish title). However, although food caching has been described for both the European Nuthatch (Löhrl 1958, Moreno et al. 1981) and several Asian (Löhrl 1988) and North American species (references in Vander Wall 1990), these studies have used artificial foods (sunflower seeds) normally not available in the habitats that nuthatches inhabit. The provision of artificial food such as sunflower seed no doubt is a valid method for answering certain specific questions relating to food storing. However, one must be aware of the fact that the pattern of storing that the birds employ may differ from the one they use when storing naturally occurring food, e.g. storing niches may differ.

The present paper aims at giving a descriptive account of the storing behaviour and cache sites used by European Nuthatches in natural conditions.

Study area and methods

Observations were carried out in Dalby Söderskog National Park, a 36 ha mixed deciduous wood 10 km east of Lund, southernmost Sweden (55°40'N, 15°20'E). This wood has been left largely unmanaged and contains numerous fallen trees and much dead wood. Although in a process of natural change, with the oldest tree generation gradually becoming replaced by younger trees, the wood still contains plenty of old oak *Quercus robur,* beech *Fagus sylvatica* and elm *Ulmus glabra* trees. Some dryer areas are dominated by beech, but most of the wood is truly mixed. Most often there is a predominance of elm, but with a high proportion of oak and beech and also with scattered ash *Fraxinus excelsior* trees. Beech-dominated and many elm-dominated parts are rather open whereas richer areas with more oak have an understorey of hazel *Corylus avellana;* other areas have regenerating very young ash. In mast years, solitary beech trees scattered throughout the wood, some of them very old, produce heavy crops and these trees tend to produce some mast also in less good years. Because of airborn pollutants, lichens are scarce on trunks and branches contrasting with the situation elsewhere in Sweden. In general the wood is fairly open thus facilitating observations of bird behaviour. Most observations of food storing by Nuthatches were made in its mixed, central parts in which the proportion of oak is relatively high.

During 1977-1991, the spring population of Nuthatches in Dalby Söderskog has varied between 4 and 20 pairs, in relation to the severity of the preceding winter (unpubl. data); the autumn population, although not censused, no doubt has been considerably larger on average (cf. Matthysen 1989, Enoksson 1990). The caching behaviour of Nuthatches exploiting natural foods was studied from autumn 1979 onwards, with more systematic observations in 1979, 1980, 1986 and 1992. Observations of retrieval and use of stored food were made in six winters during 1979/80 to 1986/87. In addition, a very limited experiment in which sunflower seeds and commercial hazel nut kernels were provided, was carried out in early spring 1980.

To characterize the kind of sites used for caching, I located Nuthatches either when they were actively storing food or followed them until they started doing so. I then recorded the kind of food stored and of cache site used (ground, fallen log, tree, or other), estimated height above ground and, for trees, species, diameter of trunk or branch used. I also noted other characteristics of the cache site, such as whether in moss or rotten wood. In some data sets I also recorded whether beech nuts were shelled or not before being cached, and whether or not caches were covered. On a number of occasions I also recorded the time taken to store an item (and the time taken to find a new one). All observations were continuously talked into a small, portable tape recorder.

Nuthatches live in permanent pair territories (e.g. Löhrl 1958, Matthysen 1986, 1987), and even though birds sometimes flew considerable distances intruding into the territory of another pair in order to exploit a particularly rich source of food (as below an old beech), this meant that I usually recorded the caching activity of just one pair at a time. However, data were collected from many pairs over several years and I have been unable to find any significant differences in the kind of sites used by different pairs, so I am confident that the data presented below give an adequate description of the caching behaviour of Nuthatches in old, mixed deciduous forest.

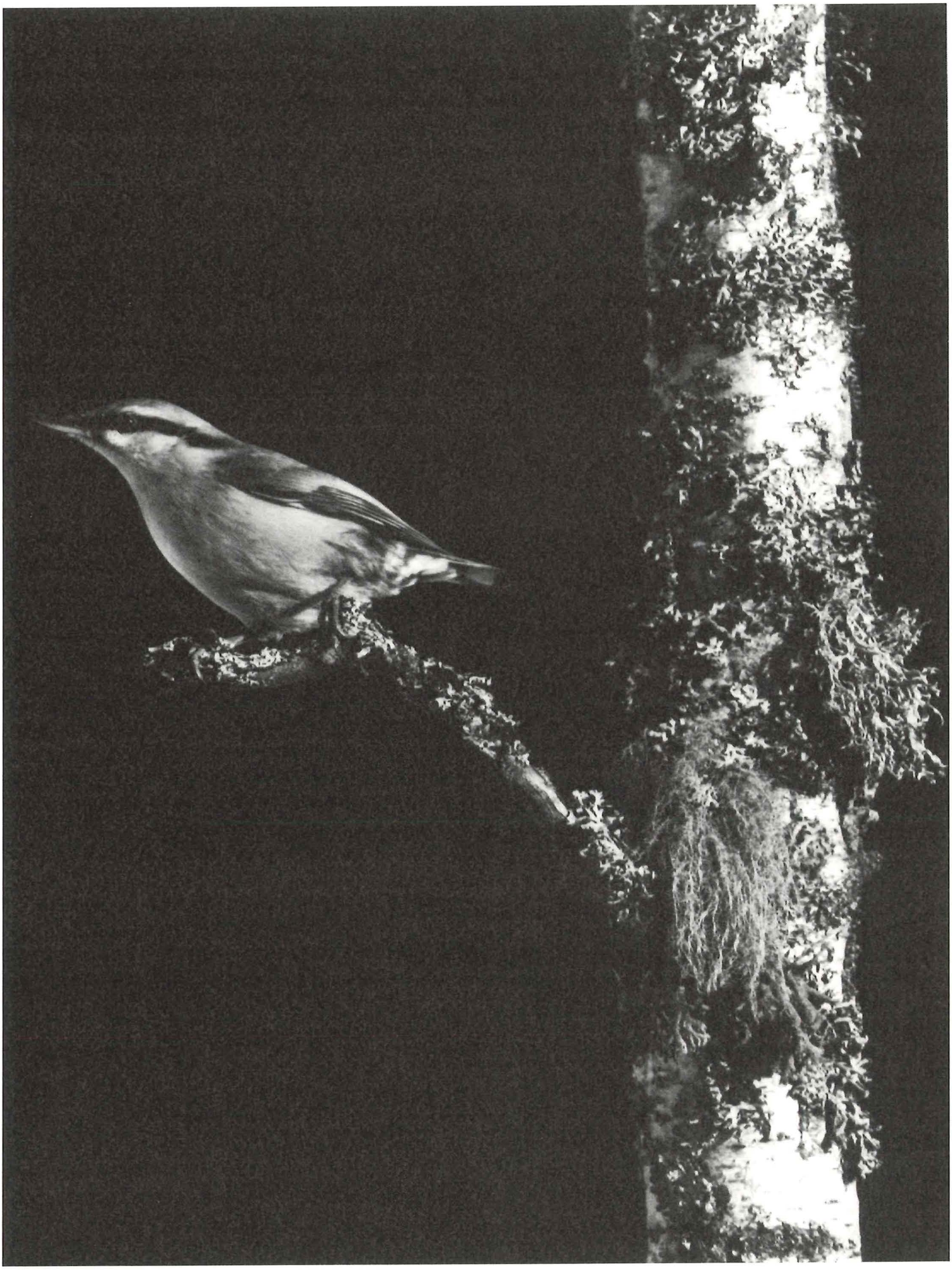
In five winters I followed the foraging activities of Nuthatches in mid-winter in order to estimate how often they retrieved, and used, cached beech or hazel nuts. After locating a Nuthatch or, usually, a pair of Nuthatches, I tried to keep one or both birds under continuous surveillance for as long a period as possible (up to 46 min) recording each time they recovered a nut. Nuthatches are easier to find when they hammer a nut open than when they forage; when Nuthatches were found in this way, observations were not started until normal foraging had been resumed for a couple of minutes.

Caching behaviour

Seasonal occurrence and kinds of food cached

Nuthatches cache food year-round. Although my observations between late April and mid-October are only casual, I could demonstrate caching on 21 May 1980, i.e. when Nuthatches in South Sweden have young in the nest, by providing mealworms to one pair; the male took 3-4 mealworms at a time and cached them singly in trees. I have also seen a male Nuthatch cache some kind of nut in early June and a female cache a large larva in late summer. In early August 1988, when ants were swarming in a small village, I observed a pair of Nuthatches catching them on the wing, eating some and caching others in fruit trees (cf. Dorka 1980). Also in winter and early spring have I seen Nuthatches cache insects (a larva, a moth and a carabid beetle, respectively). However, no doubt caching activity peaks in autumn when first hazel and later beech nuts become available.

Hazel nuts seem to be collected and cached from August onwards as long as they remain available, but, at least in Dalby Söderskog, caching birds are extremely difficult to observe in early autumn because of the dense vegetation in parts with hazel. Beech nuts are taken as soon as they can be extracted from



The food caching European Nuthatch *Den födohamstrande nötväckan.* Foto: Jan Schutzer the cupulae. After a long drought in summer 1983, a heavy mast year, branches on a beech tree had partly wilted making the cupulae open earlier than normal. Thus already on 19 August a pair of Nuthatches were busy caching beech nuts. Usually, however, the caching of beech nuts started in late September. At this time the Nuthatches either ran outwards on the finer twigs or hovered in front of them inserting their long bills into the cupulae and extracting a nut. As more mast fell to the ground later in the season, Nuthatches spent increasingly more time searching for seeds there.

General behaviour during caching

Nuthatches are scatter-hoarders, i.e. cache items singly scattered over the territory (Löhrl 1958, Persson et al. submitted). Löhrl (1958) has provided a detailed description of the caching act of Nuthatches. In short, a beech nut is usually carried to a tree and either shelled or cached with the shell intact (see below). Whether shelled or not, it is inserted deep into a crevice, moss or rotten wood. Especially when placed in rotten wood or a crack in a dry branch, the nut is often hammered in place. In most instances, the cache is then covered with a tuft of moss, dead wood, or some other material available within the nearest few decimetres of the bird. After a quick inspection the bird leaves the site or, occasionally, removes the nut and tries to store it in another place. Sometimes as many as 4-5 sites are tried before an item is finally cached.

As described by Löhrl (1958), when smaller seeds are taken (such as sunflower seeds provided by man), Nuthatches usually take two or three seeds at a time, depositing them on a horizontal branch while caching the first one; remaining seeds are then cached within a few decimetres to a couple of metres from the first one.

The covering of caches

In the material collected in 1980-86, I had explicitly stated that the Nuthatch covered its cache in 101 out of 111 cases (91%), but no mention of whether the cache was covered or not had been made in another 115 cases. In a material collected in late autumn 1992, the cache was covered in 49 of 60 cases (82%). However, this material included seven instances when only pieces of beech and hazel nuts were cached (after partial comsumption); in four of these the cache was left without cover. Of the remaining instances when caches were not covered, two were very deep behind loose bark and in a crack in a dry branch, respectively; in one, the bird seemed to search for something to cover the cache with but found nothing; in one, it made covering movements without any material in its bill. From these data, it seems safe to conclude that European Nuthatches cover at least 80%, and probably more, of their caches of naturally occurring seeds.

Shelling of beech nuts

Often Nuthatches shell a beech nut before caching it, usually by sitting upside down on the trunk hammering on the nut, after having inserted it in a bark crevice. The frequency with which the shell is removed from beech nuts before caching clearly depends on the future cache site. Thus, whereas 74 out of 106 beech nuts cached in trees were shelled, this was the case for none of 55 nuts cached in rotten logs on the ground, in bare soil among the roots of up-rooted trees, or in the ground itself ($\chi^2 = 68.3$, d.f. = 1, $P < 0.001$). I have no data to show whether the proportion of nuts cached with the shell removed changes during the course of the autumn.

Time taken to create a cache

The mean time taken a Nuthatch to store a beech nut from leaving the source until returning to it was 65 s (SD 68 s, N = 90), with a range from 13 to 485 s. The longest caching times reflect the shelling of the nut and the trying of a large number of sites in succession. Caching in the ground was faster than caching in trees as indicated by the fact that all of nine timed caching events there involving naturally occurring food items took less than 29 s (mean 22.0 s, SD 6.26; $t = 1.89$, $P < 0.1$).

In an experiment in which sunflower seeds and hazelnut kernels were provided, hazelnut kernels took 34.2 s (SD 13.2 s, N = 11) to cache in trees and 23.9 s (SD 12.3 s, N = 16) to cache in the ground ($t = 2.08$, $P<0.05$). A caching trip with sunflower seeds took 43.9 s (SD 19.4 s, N = 45) reflecting the fact that Nuthatches normally take two or three such seeds at a time.

The time it took a Nuthatch to find a beech nut after returning to the source of course varied with the size of the beech mast crop. In 1980 it took 26 s (N=30) and in 1983, a mast peak year, 10 s (N=66). However, one must keep in mind that these figures were obtained at beech trees during peak availability of nuts.

Cache sites

Cache site characteristics

The height distribution of 206 caches for which height was recorded, is shown in Table 1. About a third of the caches were below 1 m, most of them in the ground or on fallen logs but some were in moss at the base of thick trunks. Almost half were between 5 and 15 m high up in trees (most mature trees in Dalby Söderskog approach 20 m and some exceed this height), a height distribution similar to that reported by Moreno et al. (1981) for Nuthatches caching sunflower seeds in winter.

Of a total of 348 cache sites recorded, 19.8% were in the ground, including in the soil among the roots of up-rooted trees, and another 10.6% were on fallen, usually rotten and moss-covered logs; the remaining 69.5% were in trees, including a few in hazel. More than half of those in trees (57.9%) were on either main or secondary, more or less vertical trunks, and of the 102 caches made on branches, only 18.6% were on branches less than 4 cm thick. Thus, Nuthatches mainly used trunks and thick branches for caching.

Table 2 gives a more detailed presentation of the kinds of sites used by the Nuthatches when caching in trees. Sometimes a cache site would show more than one of the characteristics listed in the table, such as moss covering rough bark. In those cases, caches were listed under the most prominent feature of the site. Most caches in holes were where small branches had fallen off but sometimes Nuthatches entered cavities and cached inside them.

Table 1. Height distribution of Nuthatch caches in Dalby Söderskog (beech nuts, N = 191; hazel nuts, N = 15).

Höjdfördelningen för 191 bokollon och 15 hasselnötter gömda av nötväckor i Dalby Söderskog.

Height (m) *Höjd (m)*	Beech nuts *Bokollon*	% %	Hazel nuts *Hasselnötter*	% %
>20	1	0.5	1	6.7
15 - 20	12	6.3	-	-
10 - 15	46	24.1	-	-
5 - 10	51	26.7	-	-
2 - 5	22	11.5	2	13.3
1 - 2	7	3.7	-	-
0 - 1	36	18.8	1	6.7
Ground (0) *Marken*	16	8.4	11	73.3

Tree species used for caching

To obtain an estimate of the species composition among trees available for caching, I counted all trees more than 20 cm in diameter at breast height within 5 m on either side of a number of random transects through those parts of the wood in which caching observations had been carried out. This distribution was then compared with that for trees used for caching, the two being significantly different ($\chi^2 = 91.1$, d.f. = 3, $P < 0.001$). Nuthatches showed a clear preference for caching in oak which was used twice as frequently as expected from its abundance. Elm was used slightly less, and beech and ash much less than expected. However, there has been no regeneration of oak in Dalby Söderskog for a very long time and so oaks are on average older and thicker than the other tree species. As elm may not be suitable as a cache substrate until mature, I made a new estimate counting only trees more than 45 cm in diameter (b.h.). Although less pronounced, the preference for oak, and the difference between observed and expected values, still remained ($\chi^2 = 19.4$, d.f. = 3, $P < 0.001$). A similar preference for caching in oak was also found by Moreno et al. (1981).

Table 2. Characteristics of Nuthatch caches in Dalby Söderskog (caches in the ground, among the roots of fallen trees, etc. excluded; N = 226 beech nuts).

Egenskaper hos 226 gömmor för bokollon (gömmor i marken, rotvältor och likn. uteslutna).

Cache characteristics *Gömmors egenskaper*	N	%
Behind loose bark *Bakom lös bark*	58	25.7
In rotten wood *I murken ved*	47	21.0
In (rough) bark *I (grov) bark*	44	19.5
In small holes *I små hål*	21	9.3
In cracks in (usually dry) wood *I sprickor i (oftast torr) ved*	20	8.8
In moss *I mossa*	15	6.6
"Dry branch", unspecified *"Torrgren", ospecificerat*	12	5.3
In fork *I grenklyka*	7	3.1
Others *Övrigt*	2	0.9

Table 3. Consumption and recaching of beech nuts retrieved during late autumn and winter, respectively.

Antal bokollon som ätits hela, delvis eller omhamstrats under senhöst respektive vinter.

Period	Eaten whole *Äts hela*	Cached after partial consumption *Äts delvis, hamstras*	Recached whole *Omhamstras hela*
Oct - Nov	2	1	8
Dec - Feb	32	6	8

One reason why Nuthatches preferred to cache in oak trees probably is that most of the oaks had plenty of dead wood (cf. Table 2). Some oaks were more or less dead while also relatively healthy ones had dead branches or stumps of branches. Although this was also true of the majority of old elm trees (and of some very old beech trees), it is probably safe to say that oaks presented more dead wood than the other species of tree. Nuthatches used dry or rotten wood extensively as caching sites. Thus, combining all kinds of dead wood, from dry branches with longitudinal cracks to rottening logs, but excluding caches made in the ground, 42.8 % (98 out of 229) of caches were in such sites.

Cache sites in relation to kind of item stored

The position of caches was dependent on the kind of item stored. While only a fifth of beech nuts were cached in the ground, 60% of whole hazel nuts were so ($\chi^2 = 16.7$, d.f. = 1, $P < 0.001$). Similarly, only three out of 57 caches of sunflower seeds were in the ground versus 13 out of 27 commercial hazelnut kernels ($\chi^2 = 24.7$, d.f. = 1, $P < 0.001$).

Use of stores

Retrieval behaviour

Nuthatches occasionally retrieved a beech nut or a piece of hazel nut during normal foraging in a way suggesting that the item was found by chance. However, when Nuthatches were observed in winter, the usual pattern was uninterrupted 'normal' foraging for tens of minutes, i.e. the chiselling off of flakes of bark, moss, etc. and the inspection of bark crevices. The focal bird would then suddenly fly directly to a particular site, for instance a rotten branch, often 10-20 m away, and start hammering. After a while it would extract a beech or hazel nut which was then either consumed partly or in its entirety. In the former case, the remains were most often cached, normally close to the place of consumption.

Frequency of retrieval

During the coldest period (Dec - Feb) in each of five winters between 1980/81 and 1986/87 I followed foraging Nuthatches and recorded each time they retrieved and consumed a nut. In total 29.9 'Nuthatch hours' and the retrieval of 73 nuts were recorded, giving an overall retrieval frequency of 2.4 nuts/h. There were, however, considerable differences between years. After the poor mast autumn of 1981, only eight retrievals were seen in 455 min (1.1 nut/h), whereas after the very rich mast in autumn 1983 five retrievals were recorded in 66 min (4.6 nuts/h).

Recaching

Retrieval of cached nuts was also commonly observed during periods when beech nuts were still available for caching (and were being cached). In such situations retrieved nuts were either eaten or recached. Recaching of stored food items occurred at all times but seemed to be more frequent in late autumn than in winter (Table 3). As during the winter observations, it was sometimes difficult to decide if a cache was found by chance during normal foraging. Mostly, however, the bird would fly to a particular site and start hammering only to retrieve a beech nut that was later cached in a new site, sometimes after first having been shelled (cf. Persson et al. submitted).

Discussion

Traditionally one distinguishes between short-term and long-term hoarding (Källander & Smith 1990, Vander Wall 1990). In the former, the stored food is used within hours or days, whereas long-term hoarding means the storing of food over longer periods of time, such as from one season to another. This distinction has, however, been criticized recently (Stanback 1991), mainly on the grounds that storage times may show continuous variation and that the two categories thus may represent only the ends of a continuum. Where then does the European Nuthatch's food caching fall?

Both this study and a previous one using artificial food (Nilsson et al. 1993) have conclusively shown that Nuthatches use hoarded food long after it was stored (also see Löhrl 1988). In the study of Nilsson et al., Nuthatches still retrieved cached sunflower seeds in late winter 98 days after the feeders had been removed, and in the present study cached beech and hazel nuts were used long after these nuts had become unavailable to non-hoarders. Thus, there is no doubt that the Nuthatch must be considered a long-term hoarder. However, long-term and short-term use of hoarded food may not be mutually exclusive even though the "goals" may differ. Thus, if short-term use is a means of avoiding carrying fat and of achieving an optimal allocation of resource intake during the course of the day (McNamara et al. 1990), the same pattern of exploitation could well apply to food stored over long periods of time. Interestingly, Nilsson et al. (1993) demonstrated that the rate at which Nuthatches retrieved and consumed cached seeds was linearly related to ambient temperature: more cached seeds were used on cold than mild days.

Do Nuthatches remember their caches?

If Nuthatches use the stores they create in autumn all through winter, how then do they relocate their caches? Some species, notably the nutcrackers *Nucifraga* spp., have been shown to possess a remarkable capacity to remember their stores (for data and references, see Vander Wall 1990). Do Nuthatches have a similar capacity? Unfortunately this question cannot yet be answered. During the winter observations of retrieval of cached food in the present study, Nuthatches were often seen to interrupt their normal foraging and fly directly to a particular spot and retrieve a nut, and similar observations were made by Persson et al. (submitted). However, as shown above, recaching of nuts was common and it is therefore impossible to say for how long a particular cache had remained unexploited. In some cases snow or ice had covered the cache for about a week, the Nuthatch removing it to reach the cache. However, conclusive evidence that Nuthatches can remember their stores over longer periods of time are lacking.

Persson et al. (submitted) speculated that by recaching the bird refreshes its memory, thereby extending the period over which stored food can be used. Another explanation of this behaviour is that the bird recaches for its own use those items cached by its mate which it happens to come across. Although this may sometimes be the case, the fact that a bird would often fly directly to a site, retrieve a nut and then recache it, speaks against this explanation. In the study of Persson et al. (submitted), recaching took significantly longer than the original caching, implying that recached seeds were more carefully hidden; no such data are available from the present study. However, on one occasion (26 October 1980, not included in the data presented above) a pair of Nuthatches were extremely busy extracting nuts from the cupulae of a beech tree. Apparently the cupulae had just opened, possibly in response to the weather conditions, and the birds only quickly inserted the nuts in the rough bark of some nearby oaks before returning to the beech canopy. It is possible that they used the oaks as a temporary storage place enabling them to secure as many of the nuts as possible before these were discovered by competitors (cf. discussion in Källander & Smith 1990, Persson et al., submitted).

Cache protection, cache sites and preparation of food to be stored

Normally the Nuthatches hid nuts carefully, indicating that they were valuable to them. Thus, more than 80% of all caches were covered with material from the immediate surroundings of the cache, and those that were not covered were usually in well-protected sites such as deep cracks in dry branches, etc. Nearly 70% of all cache-sites recorded were in trees and of these more than 40% were in dead, often rotten wood. The latter kind of substrate is probably important also in other areas (pers. obs.), but may have been more so in Dalby Söderskog where there is very little lichen growth on trunks and branches.

The kind of item to be cached influenced the choice of storing site, as shown by the fact that a significantly higher proportion of hazel than beech nuts was cached in the ground (and of commercial hazel nut kernels than sunflower seeds). Apparently the Nuthatches assessed how difficult an item was to cache - or, perhaps, how valuable it was. This observation has implications for studies of the caching niches of small birds: the use of sunflower seeds may give a picture differing from that of foods cached naturally. That is not to say that studies using sunflower seeds cannot provide interesting insights, only that some caution is necessary when interpreting the results.

The seed coat was removed from a large proportion of the beech nuts before they were cached. Thus, the birds incurred a handling cost at the time of caching (cf. Woodrey 1990) and made a similar benefit (in time saved) at the time of exploitation (when time may be more important). For this to be the explanation for shelling, then a large proportion of the nuts cached must survive until exploited by the hoarder, or the time-saving benefit must be great, or both. One might think that removal of the seed coat would reduce the nuts' resistance to fungal attack but this still remains to be tested. It is interesting to note, however, that none of the beech nuts seen to be cached in the ground, or in rotten logs on the ground, were shelled prior to caching, i.e. in places where nuts seem likely to deteriorate more rapidly than in trees. An alternative explanation for the shelling of nuts would be that shelled nuts are for short-term use whereas those cached intact are for long-term use.

The adaptive value of food caching in the Nuthatch

As indicated in this study, Nuthatches scatterhoard food year-round but do so particularly in autumn when suitable seeds such as hazel and beech nuts are available. Although estimates of the amounts stored are still lacking, the amounts are clearly impressive, especially in mast years. In the present study it took a Nuthatch on average slightly more than a minute to cache a beech nut, and observations of mine indicate that a bird may cache up to 20-30 beech nuts per hour. Hoarding may go on for much of the day in autumn, only interrupted by foraging bouts and interactions with neighbouring pairs. As beech mast may be available from the end of September well into December (unless covered with snow), these figures give a rough indication of the amounts of food stored; to these should be added hazel nuts stored from August onwards.

If Nuthatches store such large quatitites of food as suggested above and use the stores throughout winter, is this reflected in their winter survival? Or, to express the question in a more precise way: Is there a positive correlation between the amounts of food stored and winter survival in European Nuthatches? Do nuthatches that are able to store much food have better survival than those that are not? Is winter survival better after mast autumns than after autumns poor in nuts? The unexpected answer to these questions seems to be 'no'. In several studies (e.g. Nilsson 1987, Matthysen 1989, Enoksson 1990), late autumn populations of Nuthatches have been found to be higher in mast years, reflecting higher recruitment (Nilsson 1987, Enoksson 1990) or better autumn survival of juveniles (Matthysen 1989). Although spring populations were higher after autumns rich in beech mast, winter survival was uncorrelated with beech mast abundance (Nilsson 1987) or was even lower among adults after mast autumns (Matthysen 1989). Enoksson (1990) experimentally supplied sunflower seeds from summer to the beginning of December in two years with few hazel nuts. In both years, the autumn density of Nuthatches increased in her plot but winter survival was unaffected. These results may appear especially intriguing as Nilsson et al. (1993) in a study somewhat similar to that of Enoksson found a clear effect of stored food on the nutritional status of Nuthatches in winter. The most likely explanation seems to be that mortality over winter is density-dependent and masks the positive influence of stored food. However, an experimental study of the effects of food caching on Nuthatch winter survival is called for.

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Sammanfattning

Nötväckans Sitta europaea *födohamstring*

År 1897 publicerade geologen och naturforskaren A.G. Nathorst en kort uppsats kallad ”Nötväckans sädesplanteringar i träden” (Nathorst 1897). Från iakttagelser av havreplantor uppe i träden och hur sädeskornen placerats drog han slutsatsen att det var nötväckor, som åstadkommit fenomenet, och han drog också den likaledes korrekta slutsatsen att de gömt kornen för kommande behov, dvs hamstrat. Nötväckans hamstringsbeteende har sedermera beskrivits av Löhrl (1958). Hans studier, liksom senare studier av asiatiska och nordamerikanska nötväckearter (Löhrl 1988, Vander Wall 1990) har emellertid använt solrosfrön som hamstringsobjekt (vissa arter har därtill endast studerats i voljär). Föreliggande arbete beskriver nötväckans hamstring av naturligt förekommande föda, främst bokollon, under naturliga betingelser.

Studieområde, metod

Studien, som varit ganska extensiv, genomfördes i Dalby Söderskog nationalpark 10 km öster om Lund, Skåne, under åren 1979-1992, med mera intensiva insatser under vissa av åren. Vårpopulationen av nötväcka i Dalby Söderskog varierade under denna tid mellan 4 och 20 par (egna opubl. data). Höstpopulationens storlek är okänd men torde samtliga år ha varit högre, ibland mycket högre.

Även om Dalby Söderskog inte gått fri från ingrepp, har skogen ändå fått utvecklas förhållandevis fritt och det är gott om delvis döda träd, liksom av omkullblåsta träd i olika stadier av förmultning. På grund av regionens höga halter av luftföroreningar saknar träden emellertid i stort sett lavar, något som sannolikt påverkar nötväckornas val av hamstringsplatser. Skogen, som är ganska öppen, domineras av alm i de flesta områden men av bok i torrare delar. Gamla ekar är vanliga i nästan hela skogen och speciellt i dess centrala delar, där hassel utgör buskskikt. Åtminstone enstaka bokar finns inom flertalet nötväckerevir (inom samtliga studerade).

För att beskriva det slags platser nötväckorna använde som gömställen för framför allt bokollon, men även för hasselnötter, lokaliserade jag hamstrande nötväckor eller följde nötväckor tills de började göra hamstringsturer. I en kasettbandspelare talade jag in uppgifter om typ av gömställe (mark, rotvälta, liggande stock, träd, osv.), gömmans höjd över marken, och för gömmor i stammar och grenar, deras diameter. Vidare noterades detaljer som huruvida gömman var i lös ved, i mossa, grova barkspringor etc. samt, för ett stort antal gömmor, huruvida fågeln täckte över gömman innan den lämnade platsen. I samband med vissa observationer noterades också om nötväckan skalade bokollonet innan detta gömdes.

Under den kallaste delen av fem vintrar följde jag också nötväckor kontinuerligt under deras födosök under så långa sammanhängande perioder som möjligt och noterade deras utnyttjande av gömd föda.

Nötväckor håller par-revir året runt och fåglarna är oftast trogna reviret under hela sin livstid (Löhrl 1958, Matthysen 1986, 1987), men genom att studierna utfördes under åtskilliga år och i olika delar av skogen torde de insamlade data vara representativa åtminstone för nötväckor i sydsvenska lövskogar.

Resultat

Nötväckor gömmer föda året runt (egna iakttagelser), men den viktigaste hamstringsperioden infaller på hösten då först hasselnötter och sedan bokollon blir tillgängliga. De är ”gleshamstrare”, dvs placerar endast en födopartikel i var och en av glest utspridda gömmor. Vanligen täcks det gömda över med material från den närmaste omgivningen - i föreliggande studie täcktes 82-91% av alla gömmor; i de fall så inte skedde var födan (vanligen ett bokollon) placerad djupt bakom lös bark eller i djupa sprickor i ved.

Mycket ofta skalades bokollon innan de hamstrades. Intressant att notera är, att 74 av 106 bokollon som gömdes i träd skalades, till skillnad från inget enda av 55 som placerades i marken eller i ruttnande stockar.

Det tog i medeltal nötväckorna 65 s (13 - 485 s, N = 90) att gömma ett bokollon och återvända till källan. De längsta tiderna uppstod när fågeln prövade ett stort antal ställen innan den slutligen gömde. Tiden att finna ett bokollon varierade naturligtvis med tillgången och var under den rika bokollonhösten 1983 endast 10 s (N = 66), uppmätt under bokar när tillgången var som högst.

De flesta gömningar skedde på 5-15 m höjd och endast drygt 1/10 i marken (Tabell 1). I träd var mindre än en femtedel i grenar av mindre än 4 cm tjocklek, dvs nötväckorna visade en förkärlek för stammar och grova grenar. Av trädslagen, som utnyttjades för gömning, visade nötväckorna en klar (och statistiskt säkerställd, $P < 0,001$) preferens för ek, möjligen därför att ekarna i Dalby Söderskog har rikligt med döda, torra eller murkna grenar. Nästan 40% av alla gömmor i träd skedde nämligen i olika typer av död ved, följd av "lös bark", vilken också oftast är förbunden med död ved (Tabell 2). Valet av hamstringsplats var också beroende av födoslag: en signifikant ($P < 0,001$) högre andel hasselnötter än bokollon hamstrades i marken.

Under den kallaste delen av fem vintrar följde jag nötväckor och registrerade när de plockade fram hamstrad föda. Oftast skedde detta genom att de avbröt sitt normala sökande (under vilket de med näbben fläker bort mossa och lös bark, inspekterar sprickor och håligheter, osv.), flög iväg till en bestämd punkt, stundom flera tiotal meter bort, där de sedan hamrade med näbben för att efter en stund hala fram ett bokollon eller en hasselnöt. I medeltal under knappt 30 "nötväcketimmar" registrerades 2.4 sådana framplockningar av hamstrade bokollon/nötter i timmen; efter den usla bokollonhösten 1981 endast 1,1 nöt/h och efter den mycket rika hösten 1983 4,6 nötter/h.

Såväl under hamstringsperioder som under vintern omhamstrades en del av den framplockade födan, dock tydligen en mindre del under högvintern än under hösten (Tabell 3).

Diskussion

Såväl föreliggande studie som en experimentell studie av Nilsson et al. (1993) visar att nötväckan är en långtidshamstrare, dvs att den utnyttjar föda lång tid efter det att denna lagrats. Frågan är hur nötväckan återfinner sina gömmor, i synnerhet som mängden bokollon och hasselnötter som hamstras under loppet av en höst torde uppgå till åstskilliga tusen. Ännu saknas studier av nötväckans minneskapacitet, men kan den vara i närheten av nötkråkornas (se Vander Wall 1990 för data och referenser)? Persson et al.(submitted) spekulerar i att omhamstring kan vara en metod att "fräscha upp minnet".

Nötväckorna i föreliggande studie gömde bokollon och hasselnötter noggrant - mer än 80% av alla gömmor täcktes noga och dessutom var många ollon djupt inkörda i murken ved, djupa sprickor och liknande, något som antyder att den gömda födan var värdefull.

Det faktum att en högre andel hasselnötter än bokollon gömdes i marken visar att hamstringsplatserna anpassas till födoslaget. Denna iakttagelse har en viss betydelse: försiktighet är påkallad när det gäller vissa slutsatser baserade på experiment med solrosfrö.

En hög andel av bokollonen skalades innan de gömdes, vilket innebär att fågeln ådrog sig en (tids)-kostnad i samband med gömningen. Sannolikt mer än kompenseras denna av den tidsvinst fågeln gör vid utnyttjandet (då tid kan vara än viktigare än vid hamstringstillfället). Man tycker dock att skalade bokollon skulle vara mer utsatta för svampangrepp än oskalade, men detta återstår att undersöka. Intressant är dock att konstatera att bokollon som gömdes i mark och liknande ställen, där risken för svampangrepp förefaller vara högre än uppe träden, aldrig skalades.

Om nu nötväckan är en långtidshamstrare som lägger upp stora förråd, avspeglas detta i högre vinteröverlevnad? Eller riktigare uttryckt, står vinteröverlevnaden i relation till mängden hamstrad föda? Trots att Nilsson et al. (1993) fann att nötväckepar, som gavs möjlighet att hamstra stora mängder solrosfrön, var i bättre kondition under senvintern än kontrollfåglar som inte utfodrades, har hittills utförda studier inte visat några effekter på vinteröverlevnaden (Nilsson 1987, Matthysen 1989, Enoksson 1990). Sannolikt beror detta på att nötväckepopulationerna under höstar med rik bokollontillgång är mycket höga och att täthetsberoende vinterdödlighet maskerar de positiva effekterna av hamstring.

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Differences in bird habitat quality between plantations of Scots and Lodgepole Pine measured in terms of Pied Flycatcher *Ficedula hypoleuca* breeding success

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Abstract

The breeding density and reproductive performance of Pied Flycatchers *Ficedula hypoleuca* inhabiting nest boxes were studied in ca. 20-year-old plantations in Sweden of two pine species: the native Scots Pine *Pinus sylvestris* and the introduced North American Lodgepole Pine *P. contorta*. The analyses are based on data from 35 nest boxes placed within each of three Scots Pine and three Lodgepole Pine plantations. The plantations were distributed pairwise at each of three different sites. During the 4-year study (1989-1992), a total of 126 and 107 clutches were found in Scots and Lodgepole plantations, respectively. There was no significant difference in number of breeding pairs between the two types of pine plantations. However, reproductive success, as regards number of nestlings, tended to be higher in Scots than Lodgepole Pine habitats, and clutch size was significantly larger in Scots Pine plantations. Flycatcher food abundance in the trees was indexed by measuring insect larval droppings under pines during the nestling period in 1989. There were no significant differences in number of droppings between the habitat types. Although the Pied Flycatcher clutch size was higher in the Scots Pine habitats, it did not result in a higher number or weight of nestlings. Our results indicate that this was due to a high within-habitat and between-site variation in flycatcher breeding success. The reasons for these variations are discussed.

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Introduction

The Lodgepole Pine *Pinus contorta* was commercially introduced into Swedish forestry during the end of the 1960's (Hagner 1985). About 540 000 ha of Swedish forest land is now planted with this North American species. In some areas it constitutes more than 10% of all coniferous trees (Skogsstyrelsen/Swedish Forestry Board 1992). Since Lodgepole Pine is currently the third most common of the managed coniferous species in Sweden, many forest animals are now faced with a new type of habitat. This fact has raised concerns regarding the ability of animals adapted to the original forests to cope with this change in habitat type. Invertebrate biomass is generally lower on an introduced tree species than on native ones (Southwood 1977). This relationship also seems to apply to the introduced Lodgepole Pine in Sweden and the habitat it creates (Kardell *et al.* 1989, Sjöberg 1989, Sjöberg & Pettersson, unpubl. data), although some invertebrate species, e.g. the Pine-flower Weevil *Anthonomus phyllocola,* have adapted well to the new host (Pettersson 1992).

Mean clutch size in the Pied Flycatcher *Ficedula hypoleuca* has been reported to differ between habitats (for review, see Gezelius *et al.* 1984, Lundberg & Alatalo 1992). This difference has been attributed to variation in breeding density (e.g. Curio 1959, Lundberg *et al.* 1981, but see also Järvinen & Tast 1980), laying date, adult size and age, female weight, and frequency of polygyny. However, all of these factors might be related to habitat quality (e.g.

food abundance). For example, differences in the clutch size of birds, the mean weight of young, population density, etc., are normally higher in deciduous forest than in coniferous forest (Alatalo & Lundberg, 1984a, Alatalo *et al.* 1985, Lundberg & Alatalo 1992). Consequently, if differences in food abundance also occur between different types of coniferous forest, one would expect to find corresponding habitat-related differences in the breeding success of the Pied Flycatcher.

It seems reasonable to assume that the food availability for insectivorous birds is lower in introduced Lodgepole Pine compared to native Scots Pine *P. sylvestris* (cf. Southwood 1977). If this is the case, Lodgepole Pine plantations should have a lower habitat quality and the reproductive performance of the Pied Flycatcher should be lower than in plantations of Scots Pine. To test this we compared the average reproductive performance of the Pied Flycatcher over a 4-year period in equally-aged plantations of Lodgepole and Scots Pine at three sites. In both types of plantations nest boxes were available in excess. We also indexed one aspect of habitat quality for the flycatchers, namely the abundance of potential food items, by measuring the number of insect larval droppings (cf. Morris 1949, Tenow & Larsson 1987) from the pine trees at three sites during one of the study years.

Study area

The pine plantations are situated in central Sweden, between 61° and 63° north latitude. They were all planted between 1970 and 1972, and arranged in such a way that a *sylvestris* and a *contorta* plantation were situated side by side, creating similar conditions with regard to soil and climate, thus enabling paired comparisons. Each of the plantations was about 20 ha in size. The trees in the Scots Pine plantations are now about 8 m high, the fast-growing Lodgepole Pine about 10 m. The Lodgepole Pine allows less light to reach the ground, which may influence the field and bottom layer of vegetation, and thus potentially the abundance of insects.

Three sites, each with a pair of plantations, were selected to index insect larvae abundance. These sites, together with an additional pair of plantations of similar kind, were used to study the reproductive success of the Pied Flycatcher. However, at one of these sites Pied Flycatchers did not start to breed until 1992 (only two nest boxes occupied), and this site (which corresponds to experimental plantation 14, belonging to "Svenska Cellulosa Aktiebolaget", SCA) was therefore not included in the analysis.

Although the plantations were similar regarding the above-mentioned conditions, there were some differences: At site 1 most deciduous bushes had been removed, thus the proportion of this vegetation type, which consisted mainly of birch *Betula spp.*, was lower there than in the other plantations. At site 2 there were some wetter patches, particularly in the Lodgepole plantation, where seedling survival had been poor. This site also had a higher proportion of deciduous trees, particularly birch, than the other sites. Site 3 differed in that the pine seedlings were planted close to each other along two rows, but with comparatively long distance to the next pair of rows (Sites 1, 2 and 3 correspond to SCA's experimental plantations 2, 12 and 19, respectively.). Of the larval dropping sites, I and II corresponds to nest box sites 1 and 2.

Material and methods

In each of the six plantation stands 35 wooden nest boxes with an entrance diameter of 30 mm were distributed over the central part of the area, 50 m apart from each other, during spring 1989, well before the arrival of the Pied Flycatcher. The nest boxes were checked twice per breeding season: at the first inspection the clutch size was recorded, and at the second inspection, conducted just before fledging, the nestlings were counted and weighed. However, in 1992 the nest boxes were visited only once (when we weighed the nestlings) and this year's clutch size was estimated by adding the number of nestlings and infertile eggs in the nest. The age of nestlings when weighed differed somewhat between years, owing to variation in start of breeding, which we were not able to totally compensate for when estimating the proper time for weighting the nestlings. They were weighed on a digital balance to the nearest 0.1 g.

In total ten clutches were deserted. Of these four clutches consisted of clutches with only one or two cold eggs. These were regarded more as breeding attempts, and hence excluded from the statistical analysis. Six deserted clutches with an apparantly normal number of eggs were, however, included.

Insect larval droppings were used as an indirect measure of insect larvae abundance in the plantations (cf. Morris 1949, Tenow & Larsson 1987). In each of the stands ten square pieces of masonite (25x25 cm) were covered with a thin layer of a glue (Hernia 4286) and placed on a stick about 1 m above ground and 1 m from the trunk of a pine tree. The plates were distributed systematically throughout the plantation by placing them 50 m apart in lines. They were set out on 20 and 21 June 1989. The plates were brought into the laboratory after two weeks and the number of larval droppings were counted. We separated droppings from the following species/species groups: the Pine-flower Weevil *Anthonomus phyllocola,* and caterpillars of Lepidoptera and sawflies (Hymenoptera: Symphyta). Droppings from orders with very small insects, such as Psocoptera and Aphidoidea, were not counted.

Statistical analysis

The aim of this study was to test if there exists a general difference in habitat quality between 20-year-old plantations of *P. sylvestris* and *P. contorta.* Thus, taken this approach, differences for single years may exist, but if there is a general difference this should be detectable as a higher average value of the pied flycatcher reproductive success over a longer period of years. Otherwhise one habitat is not superior to the other in the long run. We therefore calculated annual means for the Lodgepole and Scots Pine plantations, respectively, at each site, giving four year-values for each habitat at each site. Since we wanted to test the *general* effect of habitat quality and to avoid pseudoreplication (sensu Hurlbert 1984), we then calculated the average value of these four annual mean values for each habitat at each site, giving a total of six values for the whole data set. These six values were then used to analyse the general effect of habitat quality using a randomized block ANOVA with the factors habitat and site, where site was considered as a block effect.

The same randomized block ANOVA was used to test the general effect of habitat (Lodgepole and Scots Pine) on the abundance of larval droppings. This analysis was based on mean values for each habitat at each site (total N = 6).

All analyses were conducted with the SAS statistical package. For the analysis of variance the assumption of homoscedasticity was tested by plotting residual values against both factors and predicted values. We used the Shapiro-Wilk's test to check the assumption of normality. In the dropping analysis, the sawfly larvae *Anthonomus* and "total number" of droppings were log-transformed before analysis (Zar 1984). When a significant effect of site was found, we assessed differences between sites using the Tukey test (alpha = 0.05, df = 2).

Results

The Pied Flycatcher

If differences in habitat quality exists between the Scots and Lodgepole Pine plantations, habitat should significantly explain variation in reproductive success of Pied Flycatchers. The total number of breeding pairs of Pied Flycatcher within the three sites during the period 1989-1992 was 126 and 107 in Scots Pine and Lodgepole Pine, respectively (Table 1). Habitat did not significantly explain the variation in the number of breeding birds, i.e. the breeding density of Pied Flycatcher (Table 2, Fig. 1a). However, habitat had a significant effect on the mean number of eggs in the clutch (Table 2). Although the mean number of eggs in the clutch varied considerably between sites for each habitat type, the clutches were larger in the Scots Pine habitat than in the habitat of Lodgepole Pine (Fig. 1b). This relationship between the habitats was evident for most of the years at each site (Table 3). Also the factor site contributed significantly to explain variation in clutch size (Ta-

Table 1. Mean weight (±1 S.E.) of Pied Flycatcher nestlings, number of unhatched clutches, number of deserted broods and number of broods which had left the nest boxes by the time of weighing, in plantations of Scots Pine and Lodgepole Pine, respectively. N=Number of weighed clutches.

Medelvärden för kullvikt och dess spridningsmått (± 1 S.E.), antal ännu ej utkläckta kullar (No. unh.), antal övergivna kullar (No. des.) och antal utflugna kullar (No. left).

	Pinus sylvestris						*Pinus contorta*					
Year	N	Weight	S.E.	No. unh.	No. des.	No. left	N	Weight	S.E.	No. unh.	No. des.	No. left
1989	14	12.9	0.8	1	0	0	16	13.2	0.8	1	0	1
1990	21	13.4	0.3	0	0	7	25	13.2	0.3	0	1	6
1991	38	9.1	0.6	3	3	0	22	10.7	0.6	3	3	0
1992	35	11.5	0.6	3	1	0	27	13.0	0.5	2	0	0

Table 2. Summary of randomized block ANOVA:s for the breeding success of Pied Flycatchers in the two habitats, Lodgepole Pine and Scots Pine plantations. Site was analyzed as a block effect.

Sammanfattning av ANOVA upplagd som ett randomiserat blockförsök för olika häckningsvariabler hos svartvit flugsnappare i planteringar av contortatall och tall.

	$MS_{habitat}$	df	p	MS_{site}	df	p	MS_{error}	df	R^2
No. of breeding pairs *Antal häckande par*	3.760	1	0.590	2.542	2	0.785	9.292	2	0.322
Clutch size *Kullstorlek*	0.079	1	0.009	0.105	2	0.006	0.001	2	0.995
No. of hatched eggs *Antal kläckta ägg*	0.051	1	0.418	0.135	2	0.270	0.050	2	0.763
No. of fledglings *Antal ungar*	0.092	1	0.159	0.123	2	0.134	0.019	2	0.899
Total weight of brood *Kullens totalvikt*	2.266	1	0.800	62.203	2	0.304	27.151	2	0.700
Mean brood weight *Kullens medelvikt*	0.274	1	0.548	0.212	2	0.716	0.534	2	0.395

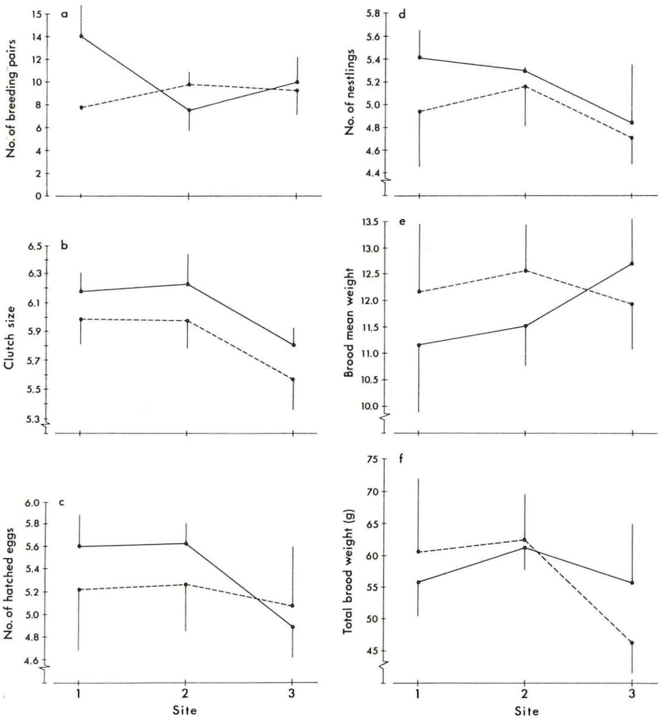

Fig. 1. Clutch size and reproductive success of the Pied Flycather utilizing nest boxes placed in plantations of *Pinus sylvestris* (solid line) and *P. contorta* (broken line) from three different sites/localities in central Sweden. Each data point is based on mean year values for each plantation during the years 1989-1992; the vertical line represents one S.E. of the mean. Site 1 corresponds to SCA's experimental plantation 2, site 2 to plantation 12 and site 3 to plantation 19. a) number of breeding pairs, b) mean clutch size, c) mean number of hatched eggs, d) mean number of nestlings, e) mean brood weights in gram, and f) mean of total brood weights in gram.

Kullstorlek och häckningsframgång hos svartvit flugsnappare i planteringar av tall (heldragen linje) och contortatall (streckad linje) från tre olika lokaler i södra Norrland. Varje punkt består av ett medelvärde från varje plantering från åren 1989-1992 (N=4). Den vertikala linjen visar medelvärdets spridning (± 1 S.E.). Lokal 1 är SCA:s försöksplantering nr 2, lokal 2 försöksplantering nr 12 och lokal 3 försöksplantering nr 19. a) antal häckningar, b) antal ägg i kullen, c) antalet kläckta ägg, d) antal ungar i kullen, e) medelvikten hos kullen i gram, och f) medelvärdet av den totala kullvikten i gram.

Table 3. Mean values (± 1 S.E.) of clutch sizes during the study period 1989-1992. N=233.

Medelvärden för kullstorlekar och spridningsmått (± 1. S.E.) under perioden 1989-1992.

	Pinus sylvestris			*Pinus contorta*		
Year	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
1989	6.0±0.3	5.7±0.3	5.8±0.9	6.3±0.4	5.8±0.4	5.3±0.3
1990	6.5±0.2	6.4±0.2	5.9±0.2	6.3±0.3	6.4±0.3	6.2±0.2
1991	6.0±0.2	6.7±0.3	6.1±0.2	5.6±0.2	6.2±0.3	5.3±0.2
1992	6.1±0.1	6.2±0.4	5.5±0.3	5.8±0.3	5.6±0.4	5.5±0.3

ble 2), and site 3 had significantly lower mean clutch size compared to both site 1 and 2 (Fig. 1b).

There was a tendency, although non-significant, for a higher average number of nestlings during the four year period in the Scots Pine habitat as compared to the Lodgepole Pine habitat (Fig. 1d, Table 2). Other breeding success parameters, i.e. number of hatched eggs, brood mean weight and total brood weight, were not associated with habitat type (Table 2). These variables also showed a high within-habitat variation as well as a high variation between sites (Fig. 1c, e and f).

Pied Flycatchers started to breed earlier during the second year (1990), and thus some broods had already left the nest boxes at the time of weighing. In that year, the number of such broods was about equally distributed between the Scots Pine and Lodgepole Pine stands (7 vs 6; Table 1). On the other hand, the spring of 1991 was unusually late, and in each of the pine plantation types, three clutches had still not hatched by the time that the birds were weighed. In 1992, three and two clutches, respectively, had not yet hatched (Table 1). Thus, we did not find any evidence for within-year differences in the time of breeding between the two pine habitats.

No predation on nestlings was observed during the study. In 1990, however, dead nestlings were found in two of the nest boxes in the Lodgepole Pine plantations. Consequently, predation on adult birds outside the nest boxes could not be excluded. This could also be the case for those clutches considered as deserted. However, in one nest box (in a Lodgepole Pine plantation in 1990) even the female was found dead, together with her brood, which might also indicate food shortage. In 1991, three clutches in each plantation type were deserted (Table 1).

Similar proportions of male Pied Flycatchers were present at the nest boxes in the two pine habitat types. In 1992, males were present at 53% of the nest boxes with broods in the *P. sylvestris* plantations, and at 71% in the *P. contorta* plantations. The difference was not statistically significant (T = 1.29, p = 0.325, df = 2, paired t-test on arcsin-transformed values, see Zar 1984).

Larval droppings

Droppings from the Pine-flower Weevil and sawfly larvae dominated while lepidoptera larvae droppings were rare. However, habitat had no significant effect on the number of droppings from these insects or on the total number of droppings (Table 4). Except for site I the *contorta* plantations tended to have higher number of droppings (Fig. 2). The Scots Pine plantations showed a low within-habitat variation, while the opposite was true for the Lodgepole Pine plantations (site III tended to have higher number of droppings, Fig. 2).

Discussion

A female Pied Flycatcher apparently selects a male depending on the quality of the nest site he offers, whereas the characteristics of the male itself seems to be of secondary importance (Askenmo 1984, Alatalo *et al.* 1986, Slagsvold 1986). The Pied Flycatcher defends the nest box area (von Haartman 1956, Harvey *et al.* 1988), but not the feeding area around the box. Still, a flycatcher is likely to forage close to its nest site, where it collects food items from the air, branches or trunks of trees, or from the field- and bottom-layer vegetation (e.g. von Haartman 1954, Alatalo & Alatalo 1979, Atlegrim 1992). Since flycatchers are not likely to forage very far from the nest site, differences in food abundance between different habitat types should be reflected in habitat-related variation in breeding phenology and reproductive performance. Sometimes, however, the flycatchers fly to more distant areas to forage (pers. obs.). Thus, such a bird species may not be the most suitable one for testing habitat quality (for example, biomass of available invertebrate food)

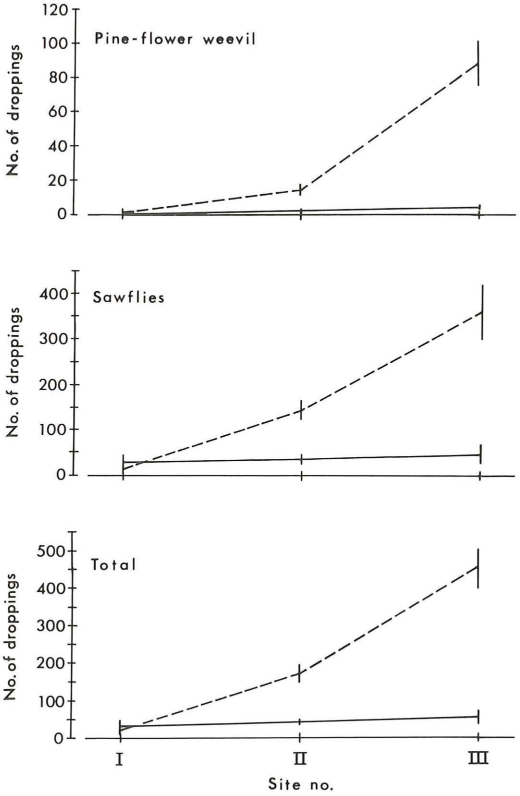

Fig. 2. Mean number of droppings from larvae of Pine-flower Weevil, sawflies and total (also including a small number of droppings from Lepidoptera larvae) on plates placed under trees in plantations of *Pinus sylvestris* (solid line) and *P. contortra* (broken line). Mean values from ten plates in each stand; the vertical line represent one S.E. of the mean. Sites I and II corresponds to SCA's experimental plantations 2 and 12, i.e. no. 1 and 2 in Fig. 1, while site III corresponds to experimental plantation no. 14.

Medelvärdet av antalet spillningar från tallblomvivel, växtstekellarver och totalt (d v s spillning från tallblomvivel och växtstekellarver samt ett fåtal spillningar från mätarlarver) som hamnat på plattor försedda med lim placerade under träd i planteringar med tall (heldragen linje) och contortatall (streckad linje). Medelvärden, samt spridningsmått (± 1 S.E.) från tio plattor i varje plantering. Lokal I och II motsvarar nummer 1 och 2 i Fig. 1, d v s SCA:s försöksplanteringar nummer 2 och 12, medan lokal III motsvarar försöksplantering nummer 14.

Table 4. Summary of randomized block ANOVA:s for mean number of insect larvae droppings in the two habitats, Lodgepole Pine and Scots pine plantations. Site was analyzed as a block effect. All variables except the mean number of Lepidoptera droppings were log-transformed according to log (y+1) before entering analysis (c.f. Zar 1984).

Sammanfattning av ANOVA upplagd som ett randomiserat blockförsök för medelvärden av insektsspillning från larver i planteringar av contortatall och tall. Lokal analyserades som en blockeffekt. Alla variabler utom medelvärdet av spillning från Lepidoptera logtransformerades enligt log(y+1) innan analysen utfördes (jfr. Zar 1984).

	$MS_{habitat}$	df	p	MS_{site}	df	p	MS_{error}	df	R2
Lepidoptera *Fjärilar*	18.03	1	0.234	14.06	2	0.310	6.33	2	0.78
Symphyta *Växtsteklar*	1.12	1	0.415	0.81	2	0.374	1.08	2	0.69
Anthonomus *Tallblomvivel*	4.21	1	0.133	3.21	2	0.179	0.70	2	0.88
Total *Summa*	1.60	1	0.307	1.57	2	0.354	0.86	2	0.73

within a particular habitat type. Nevertheless, if the birds regularly collect food at some distance from the defended territory, it should result in a higher energetic cost, compared with birds collecting food in the vicinity of the nest boxes (unless the former select more valuable food; cf. Lifjeld & Slagsvold 1988).

Alatalo *et al.* (1985) regarded food abundance to be one of the most important habitat selection criteria used by Pied Flycatchers. Their strongest evidence supporting this view is that even when the number of nest cavities is not limiting, breeding density is markedly lower in coniferous than in deciduous forest. When nest boxes are provided in excess, the population increases up to a limit which is probably determined by the food supply (Alatalo *et al.* 1985).

In our four-year study period, the clutch size was significantly affected by habitat type. Larger clutches, was found in the Scots Pine plantations (Table 2, Fig. 1b). The most probable reason for this is a difference in food abundance between the habitats. Invertebrate biomass is generally lower on introduced tree species than on native ones (Southwood 1977), but in our study the number of droppings from insect larvae collected during the nestling period did not differ between habitats (Table 2, Fig. 2). Note, however, that only two of the sites where dropping data was collected are congruent with the three sites where bird breeding success was studied. Even if there had been a significant effect of habitat on number of larval droppings, it is not probable that the dominant larvae (*Anthonomus phyllocola*) are available for the Pied Flycathers as they live more or less hidden in the pine flowers. Further, the second most common insect larvae group, the sawflies, defend themselves against enemies by synchronized movements and by producing oral effluents (Björkman 1991, p. 9; see also Hanski 1987), and is probably also of low value to the birds.

Our indirect measure of habitat quality with respect to food availability only included measures of insect larvae living in the pine trees. It can not be excluded that differences still exists between the two habitats if there are differences in density of deciduous trees, insect availability in the air, the field and/or ground layer. There is some evidence that this may be the case (Kardell *et al.* 1989, Sjöberg 1989, Danell & Sjöberg 1993, Sjöberg & Pettersson, unpubl. data).

The larger clutch size and the assumed higher food abundance in Scots Pine plantations lead to the expectation of a higher reproductive success in this habitat compared to Lodgepole Pine plantations. Contrary to expectation, habitat quality did not have any effect on the number of hatched eggs, the number of nestlings, the mean brood weight or the total brood weight (Table 2, Fig. 1c-f). The reason for this may be that there exist a difference in habitat quality just during the egg laying period, but not during the Pied Flycatcher nesting period. However, our results indicate that a high within-habitat variation and high variation between sites for bird reproduction parameters may be the reason for lack of a significant effect of habitat quality for these parameters (see Fig. 1c-f).

Beside habitat, site also contributed significantly to explain variation in clutch size and site 3 had significantly lower clutch sizes compared to both site 1 and 2 (Fig. 1b). Although sites did not differ significantly, there was a tendency for lower number of hatched eggs, number of nestlings and total brood weight, but higher mean brood weight at site 3 (Fig. 1c-f). Such a pattern may be explained on the basis of the low clutch sizes at site 3. However, the low breeding success at site 3 may also be explained by a more harsh climate, i.e. more close to the mountain range, and a lower abundance of deciduous bushes compared to site 1 and 2, which could be important with respect to food availability (se above). It ought to be noted though, that the mean clutch sizes in both pine plantation types in our study are generally of the size which could be expected for Pied Flycatcher broods in the region. For example, in the vicinity of Uppsala, i.e. south of our sites, the clutch size in coniferous forest was 6.3 eggs (Lundberg & Alatalo 1992), while in spruce plantations in Scania in southern Sweden, Källander *et al.* (1987) found the mean clutch size to be 6.16, and Gezelius *et al.* (1984) 6.58. In a spruce forest in Norway the mean clutch size (pooled data) during a five-year period was 5.55-5.97 eggs, compared with 6.0-6.5 and 5.8-6.3 for clutches in the Scots Pine and Lodgepole Pine plantations, respectively, in our study. Beside depending on nest box type (Slagsvold 1987), clutch size varies condiderably between years, along latitude gradients and between habitat types (e.g. Järvinen & Väisänen 1984, Järvinen 1989, Lundberg & Alatalo 1992).

Divergence at site three also causes a high within-habitat variation. For example, the higher number of hatched eggs in the Scots Pine plantation at site 1 and 2 is changed at site 3 (Fig. 1c). The diverging habitat pattern at site 3 may be interpreted in the same way as for site 3 divergence above. However, note that the Pied Flycathcers in the Scots Pine plantations have a high loss at hatching, and almost no losses between hatching and fledgling stage. Contrary to this, losses in the Lodgepole Pine plantations is more evenly distributed among the egg, hatching and fledgling stages.

The breeding success data can be summarized as follows: Mean clutch size was higher in the Scots Pine plantations, and this may indicate higher habitat quality than in the plantations of the introduced Lodgepole Pine. Between-site variation was probably dependent on differences in the planting techniqe, thinning operations and occurrence of wet patches causing site differences in tree density, light conditions, abundance of deciduous trees, moisture conditions, etc., which may have influenced food availability for the Pied Flycatchers. Differences in climate may also to some extent explain the variation in breeding results between different sites. Also the within-habitat variation was probably influenced by light conditions, abundance of deciduous trees, etc., but could even to some extent have been influenced by differences in breeding density between different stands (cf. Askenmo 1973, 1977, Alatalo & Lundberg 1984a, 1989), which also could be explained by the same habitat quality factors.

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Sammanfattning

Skillnader i biotopkvalitet mellan planteringar av contortatall och vanlig tall mätt som häckningsframgång hos svartvit flugsnappare.

Den till Sverige införda nordamerikanska contortatallen började planteras i större omfattning i slutet av 1960-talet och början av 70-talet. Planteringarna är i stort sett geografiskt begränsade till Norrland och upptar där numera en areal omfattande totalt ca 540.000 ha. Vi har undersökt den svartvita flugsnapparens häckningsframgång i ca 20 år gamla planteringar av contortatall *Pinus contorta* med motsvarande planteringar av inhemsk tall *P. sylvestris*. I varje plantering, som var och en omfattar ca 20 ha, har vi placerat ut 35 holkar, där diametern på ingångshålet är 30 mm. I samtliga planteringar finns ett överskott på holkar. Studierna har utförts inom fyra av skogsbolaget SCA:s försöksplanteringar. Där har contortatall och inhemsk tall planterats i samma område, vid samma tillfälle och under så lika förhållanden som möjligt. Dessa parvisa försöksplanteringar, där alltså planteringar med contortatall och tall ligger sida vid sida, har utnyttjats för våra jämförande häckningsstudier. Totalt har vi använt oss av 8 planteringar; 4 med contortatall och 4 med vanlig tall. Träden är ca 8 meter höga i tallplanteringarna, och ca 10 m i de mera snabbväxande contortaplanteringarna. Genom sin snabba tillväxt sluter sig contortaplanteringarna tidigare än tallbestånden, vilket i sin tur påverkar ljusförhållanden och därmed även vegetationssammansättningen i fält- och bottenskikt. Detta, liksom förekomst av lövträd (främst björk), d v s om planteringarna är lövröjda eller inte (och hur noggrant och konsekvent de i så fall är röjda), påverkar förekomsten av potentiella födodjur för insektsätande fåglar såsom den svartvita flugsnapparen.

Häckningsresultatet har insamlats under perioden 1989-1992, alltså fyra år. Utgångspunkten för denna häckningsstudie har varit att få ett svar på frågan om det föreligger generella skillnader i häckningsframgång hos svartvita flugsnappare mellan ca 20-åriga planteringar av contorta och vanlig tall. I den statistiska analysen har vid därför använt oss av häckningsresultatens medelvärden för de fyra studieåren och vi har således i stort sett bortsett från den skillnad mellan habitaten som kan ha funnits enskilda år. Medelvärdet för den svartvita flugsnapparens häckningsframgång över de fyra studieåren analyserades för respektive plantering (totalt N=6) som ett randomiserat blockförsök med hjälp av en 2-vägs variansanalys (ANOVA), med faktorerna habitat (habitatkvalitet) och lokal (block-faktor).

Under ett av studieåren, 1989, mätte vi indirekt förekomsten av potentiella födoorganismers förekomst i tallkronorna genom att kvantifiera antalet spillningar från insektslarver. Spillningen föll ner på limförsedda plattor. Dessa var placerade under träd i planteringarna i två veckor. Insamlingsperioden sammanföll i tid med den period då fåglarna matade sina ungar. Resultaten av denna delstudie blev att inga statistiskt signifikanta skillnader mellan habitaten kunde urskiljas i antalet spillningar från fjärilslarver, växtstekellarver, eller från tallblomvivelns larver, ej heller i det totala antalet spillningar. (Fig. 2, Tabell 4).

Vår slutsats är att det i denna studie endast i ett avseende förelåg en generell, statistiskt signifikant skillnad i flugsnapparens häckningsresultat mellan vanlig tall och contorta. Kullstorleken var högre i vanliga tallplanteringar jämfört med contortaplanteringar (Fig. 1, Tabell 2). Däremot var inte antalet ungar, eller ungarnas medelvikt, skilda åt i de två typerna av plantering (Fig. 1, Tabell 2). Slutresultatet blev således att i slutet av häckningssäsongen förelåg ingen statistiskt signifikant skillnad mellan habitaten med avseende på flugsnapparnas häckningsframgång. Skillnader i förekomst av t ex lövträd och fuktstråk i planteringarna tycks ha väl så stor påverkan på häckningsresultatet som tallarten som sådan. Reservation bör dock göras för att vi ännu inte har möjlighet att mäta kvaliteten i äldre bestånd av contortatall, ej heller i senare tallgenerationers påverkan på övrig vegetation i planteringarna, som i sin tur påverkar insektsförekomst, och därmed potentiell fågelföda.

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Ageing of Tree Pipits *Anthus t. trivialis*

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Abstract

Ageing criteria in Tree Pipits *Anthus t. trivialis* were studied and photographed at Falsterbo Bird Observatory, SW Sweden, during autumn and spring migration. Several characteristics useful for ageing were found and documented. Iris colour and the pattern on the second outermost tail-feather are valid all year, while other characteristics on wing-feathers (moult contrasts, degree of wear) are valid either in autumn or in spring/summer, depending on the moult of these feather tracts. Moult and ageing criteria are briefly commented on along with some statistics.

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Introduction

The Tree Pipit *Anthus trivialis* is widely spread and fairly common in Europe (Cramp 1988, Glutz & Bauer 1988). It is a long distance migrant wintering south of the Sahara (Zink 1975). During migration it is trapped in fairly large numbers by ringers, and since it is easy to entice to the mist nets by play-back of its song from a tape recorder, the number of ringed Tree Pipits will probably increase in the future.

Recent findings on ageing of Tree Pipits are published by Svensson (1992). These criteria and some new ones are presented and shown in colour photographs of live birds in this paper. The results are part of the "Photo Project" at Falsterbo Bird Observatory (Karlsson et al. 1985).

Material and methods

The data presented in this paper were collected during 1983-92 and are based on more than 2000 Tree Pipits trapped within the standardized ringing scheme at Falsterbo Bird Observatory, southwestern Sweden. The birds were trapped during migration and thus belonging to the North European population. The major part (ca. 90%) were trapped during autumn migration (August - early September), when the Tree Pipit is one of the most numerous passerine migrants at Falsterbo.

Photos were taken of wing, tail and head in 90 specimens (Table 1). All the photos were taken with the same camera, flashes, film and background. Furthermore, notes on biometry, moult, feather patterns and iris colour were taken of these birds as well as of others.

The age codes (Table 2), moult codes and abbreviations for feather tracts (Table 3) are mainly the same as in Svensson (1992). All numbering of feather tracts is ascendent except tailfeathers, which are numbered from the middle pair outwards (1- 6). Abbreviations and numberings are combined with an underscore in order to give short and exact descriptions. For example "Greater Covert no. 8" will be expressed as "GC_8" and "Greater Coverts no. 8 to 10" as "GC_8-10".

The term "moult contrast" (Lewington et al. 1991) is used to describe the difference between feathers of two generations, where the most recently moulted appear less worn and/or differ in shape and colouration.

Naturally, the ageing criteria presented in this paper are directly applicable only when Tree Pipits

Table 1. Number of Tree Pipits photographed in different age classes.

Antal fotograferade trädpiplärkor uppdelade på åldersklasser.

	Age *Ålder*		N
Autumn *höst*	1y	1k	19
	2y+	2+	19
Spring *vår*	2y	2k	33
	3y+	3+	19

Table 2. Explanation of age codes used by (A) Svensson (1992), (B) Swedish Ringing Centre and (C) EURING.

Förklaring till ålderskoder som används av (A) Svensson (1992), (B) Ringmärkningscentralen i Sverige och (C) EURING.

A	B	C	
1y	1k	3	Bird in its first calendar year. *Fågel i sitt första kalenderår.*
2y	2k	5	Bird in its second calendar year. *Fågel i sitt andra kalenderår.*
2y+	2+	4	Bird in its second calendar year or older. *Fågel i sitt andra kalenderår eller äldre.*
3y+	3+	6	Bird in its third calendar year or older. *Fågel i sitt tredje kalenderår eller äldre.*

occur on European latitudes, and that is also why ageing is divided into "autumn" and "spring" sections.

Moult

To understand the methods of ageing and sexing on plumage characteristics, knowledge of moult patterns is important. Tree Pipits moult twice a year (Ginn & Melville 1983; Table 4). In late summer adults (2y+) moult completely (post-nuptial moult; SC), whilst juveniles (1y) moult partially (post-juvenile moult; sp). In winter, Tree Pipits of all ages moult partially (pre-nuptial moult; wp). Primaries, secondaries, primary coverts and most tail-feathers are only moulted once a year (post-nuptial). Age criteria based on these feather tracts are valid all year (autumn - next summer) while others are valid only in autumn or in spring/summer.

N.B. The data in Table 4 were collected from birds trapped at Falsterbo. Other populations may differ in the extent of partial moult (sp, wp).

Ageing in general

Ageing criteria are listed in Table 5 and shown in Plates 1-8. When combined, these criteria make correct ageing of Tree Pipits possible all year.

A watchmaker's lens (5x magnification) is of good (and necessary) help when examining plumage characters. When iris colour is studied, a watchmaker's lens with 10x magnification and daylight or a daylight fluorescent tube are required.

Table 3. Moult codes and abbreviations for feather tracts. The abbreviations are mainly the same as in Svensson (1992).

Förkortningar för ruggning och benämningar på fjädergrupper, huvudsakligen samma som hos Svensson (1992).

Abbreviation *Förkortning*	English term *Engelsk benämning*	Swedish term *Svensk benämning*
SC	Summer complete moult (post-nuptial moult)	*Komplett sommarruggning (efter häckning)*
sp	Summer partial moult (post-juvenile moult)	*Partiell sommarruggning*
wp	Winter partial moult (pre-nuptial moult)	*Partiell vinterruggning*
PC	Primary coverts	*Handtäckare*
LC	Lesser (wing) coverts	*Mindre (arm-)täckare*
MC	Median (wing) coverts	*Mellersta (arm-)täckare*
GC	Greater (wing) coverts	*Större (arm-)täckare*
P, PP	Primary, -ies	*Handpenna, -or*
S, SS	Secondary, -ies	*Armpenna, -or*
TE	Tertial (-s)	*Tertial (-er)*
TF	Tail-feather (-s)	*Stjärtpenna (-or)*

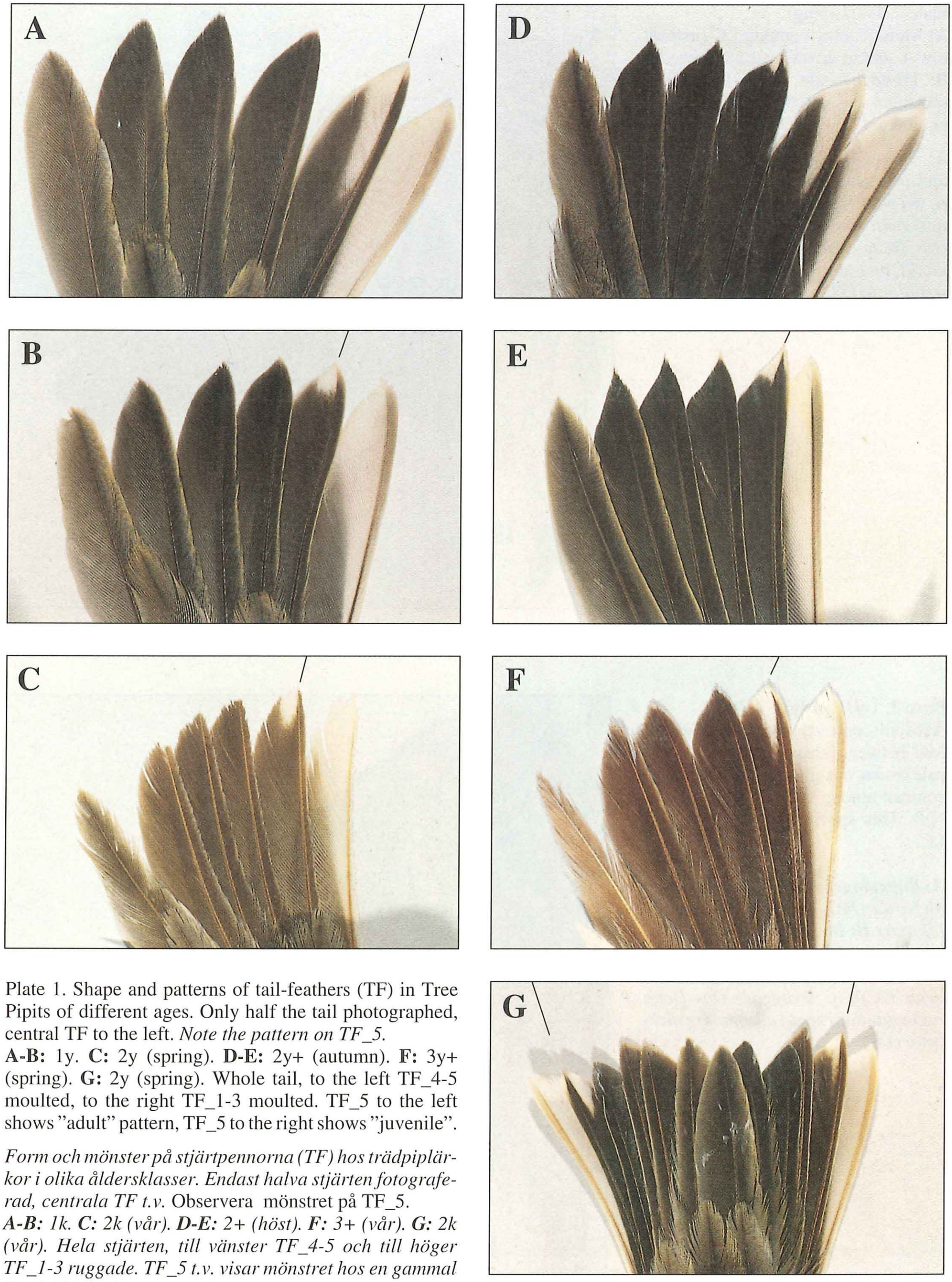


Plate 1. Shape and patterns of tail-feathers (TF) in Tree Pipits of different ages. Only half the tail photographed, central TF to the left. *Note the pattern on TF_5.* **A-B:** 1y. **C:** 2y (spring). **D-E:** 2y+ (autumn). **F:** 3y+ (spring). **G:** 2y (spring). Whole tail, to the left TF_4-5 moulted, to the right TF_1-3 moulted. TF_5 to the left shows "adult" pattern, TF_5 to the right shows "juvenile".

Form och mönster på stjärtpennorna (TF) hos trädpiplärkor i olika åldersklasser. Endast halva stjärten fotograferad, centrala TF t.v. Observera mönstret på TF_5. ***A-B:** 1k. **C:** 2k (vår). **D-E:** 2+ (höst). **F:** 3+ (vår). **G:** 2k (vår). Hela stjärten, till vänster TF_4-5 och till höger TF_1-3 ruggade. TF_5 t.v. visar mönstret hos en gammal fågel, TF_5 t.h. mönstret hos en ung.*

Plate 2. 1y/*1k* (Aug)
A: Moult contrast among LC (lowest row + one at arrowhead *unmoulted*). **B:** TE edged pale brown. N.B. This specimen has all MC, GC and TE unmoulted.

A: Ruggningsgräns bland mindre täckarna (LC) (nedersta raden samt en vid pilens spets oruggade*). **B:** Blekt ljusbruna kanter på tertialerna (TE). Obs. Detta exemplar har alla mellersta (MC) och större täckarna (GC) samt tertialerna (TE) oruggade.*

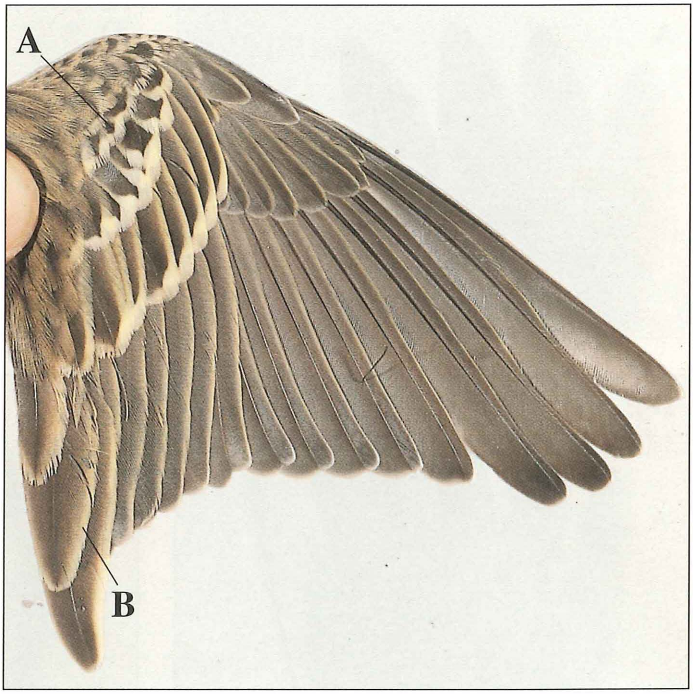


Plate 3. 1y/*1k* (Aug)
A: Moult contrast among MC (*moulted* MC between arrows). **B:** TE edged pale brown, tips slightly worn. **C:** Moult contrast among GC (GC_9 moulted). N.B. This specimen has moulted all LC.

A: Ruggningsgränser bland mellersta täckarna (MC) (ruggade *MC mellan pilarna). **B:** Blekt ljusbruna kanter på tertialerna (TE), topparna lätt slitna. **C:** Ruggningsgräns bland större täckarna (GC) (GC_9 ruggad). Obs. Detta exemplar har ruggat alla mindre täckarna (LC).*

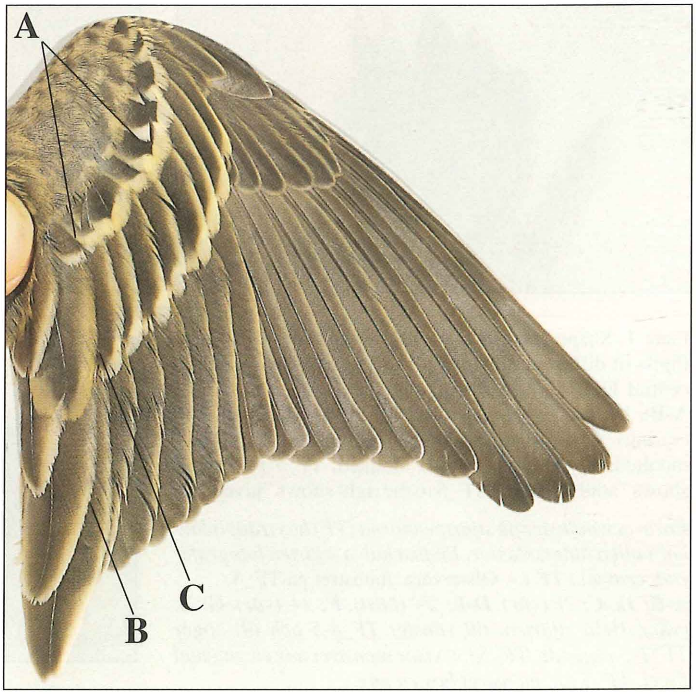


Plate 4. 2y+/2+ (Aug)
A: No moult contrasts among LC, MC or GC. **B:** TE edged brown, tips completely fresh. **C:** Inner GC *slightly* darker at tips, edges of all GC alike - cf. **3:C.**

A: Inga ruggningsgränser bland mindre (LC), mellersta (MC) eller större täckarna (GC). B: Tertialerna (TE) brunkantade, topparna helt fräscha. C: Inre GC något mörkare på topparna, men kanterna på alla GC har samma färg - jfr. ***3:C.***

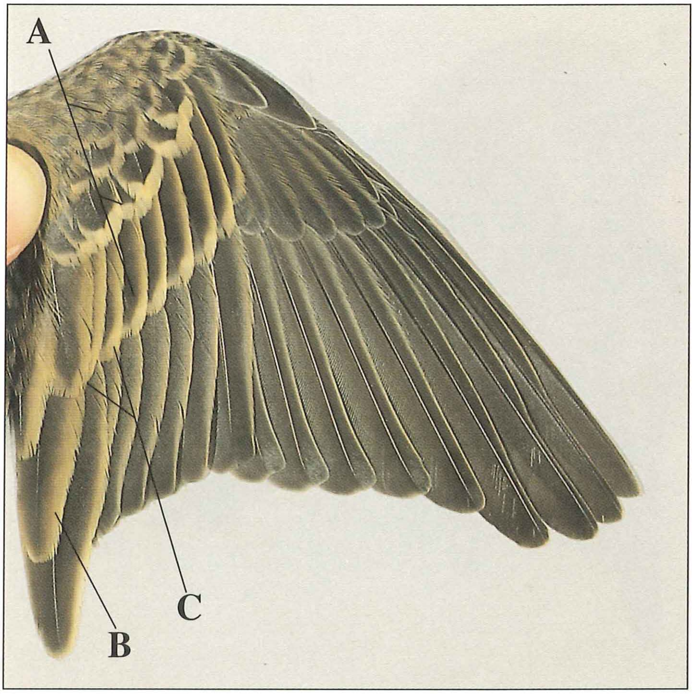
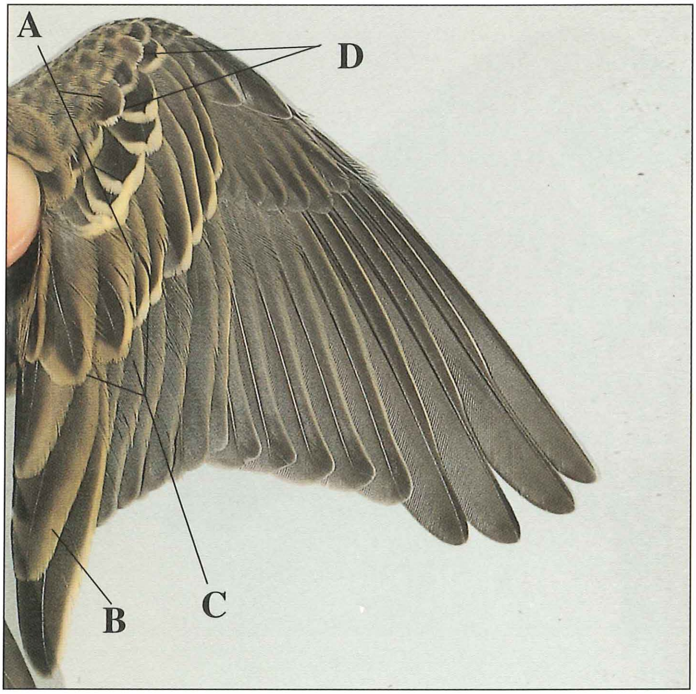


Plate 5. 4/2+ (Aug)
A: No moult contrasts among LC, MC or GC. **B:** TE edged brown, tips completely fresh. **C:** Inner GC darker at tips, edges of all GC alike - cf. **3:C. D:** Two LC not moulted during SC-moult - cf. **2:A.**

A: Inga ruggningsgränser bland mindre (LC), mellersta (MC) eller större täckarna (GC). B: Tertialerna (TE) brunkantade. C: Inre GC mörkare på topparna, men kanterna på alla GC har samma färg - jfr. ***3:C. D:*** *Två LC ej ruggade under SC-ruggningen -jfr.* ***2:A.***



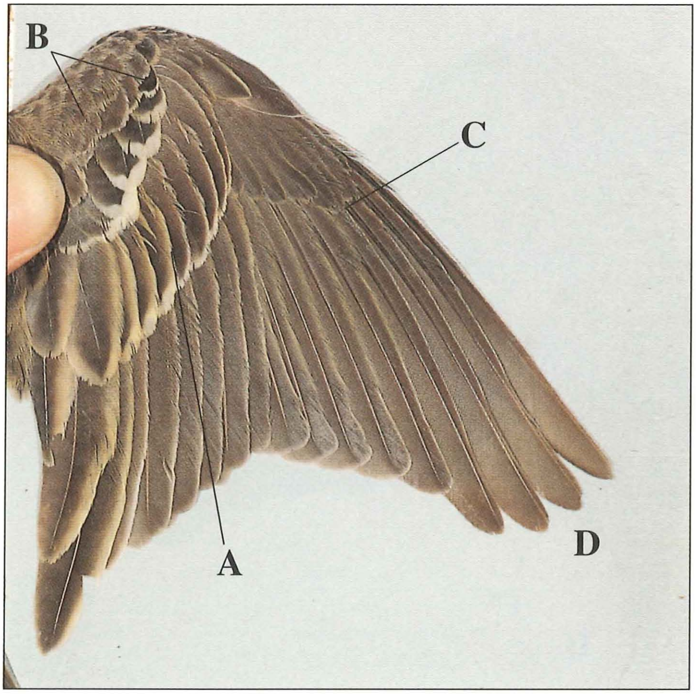


Plate 6. 2y/*2k* (Apr)
A: Moult contrast among GC (GC_5/GC_6), rather prominent, outer unmoulted GC worn. **B:** Unmoulted LC and MC worn. **C:** PC worn and with "loose structure". **D:** Tips of outer PP generally worn and bleached. Cf. Plate 7.

A: Ruggningsgräns bland större täckarna (GC) (GC_5/GC_6), ganska tydlig, de yttre oruggade GC kraftigt slitna. ***B:*** *Oruggade mindre (LC) och mellersta täckarna (MC) kraftigt slitna.* ***C:*** *Handtäckarna (PC) slitna och med "lös struktur".* ***D:*** *Yttre handpennornas (PP) spetsar vanligen slitna och solblekta. Jfr. Bild 7.*

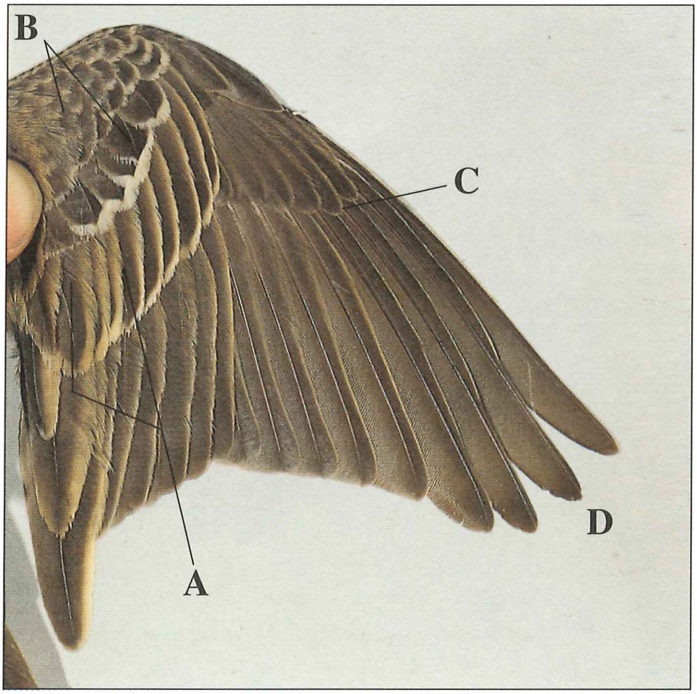


Plate 7. 3y+/*3+* (May)
A: Moult contrasts among GC (GC_6/GC_7, GC_9/GC_10), less prominent, since unmoulted GC are less worn and bleached. **B:** Unmoulted LC and MC less worn than in 2y. **C:** PC less worn and with a rather "firm" structure and contour. **D:** Outer PP generally only slightly worn. Cf. Plate 6.

A: Ruggningsgränser bland större täckarna (GC) (GC_6/GC_7, GC_9/GC_10), mindre tydlig än hos 2k (oruggade GC är mindre slitna/blekta). ***B:*** *Oruggade mindre (LC) och mellersta täckarna (MC) mindre slitna än hos 2k.* ***C:*** *Handtäckarna (PC) mindre slitna och med mera "fast" struktur och form.* ***D:*** *Yttre handpennornas (PP) spetsar vanligen lätt slitna. Jfr. Bild 6.*

Plate 8. Iris colour in Tree Pipits of different ages. A: 1y. B: 2y. C: 3y+. A slight variation occurs in 2y and 3y+.

Irisfärg hos trädpiplärkor av olika ålder. A: 1k. B: 2k. C: 3+. Viss variation förekommer hos 2k och 3+.

Autumn (after SC/sp-moult, up to wp-moult)

The pattern of the second outermost tail-feather (TF_5) is very useful for ageing, although it takes some practice to fully appreciate the differences between adults (2y+) and first year (1y) birds. First year birds (1y) have the white parts on inner webs of TF_5 less distinctly set off and generally less white on outer webs than adults (2y+), making the tip of the dark parts rather blunt in 1y and very pointed in 2y+ (Plate 1). The extension of white on inner web of TF_5 seems to be of no importance as for ageing (Plate 1).

Tips of (outer) tail-feathers are slightly worn in first year birds, already from mid-August, while adults at this time have these tips completely fresh (and generally more pointed). Naturally, adults will gradually also wear off the tips of their tail-feathers later in autumn. The wear is easy to examine when the tail is held up against a lamp or against the sky (Plate 1:A- B, D-E).

After post-juvenile moult (sp), first year birds (1y) always have two generations of wing-coverts. Moult contrasts are most frequently found among lesser coverts, sometimes among median coverts and, more rarely, among inner greater coverts (Plates 2-3). This is a safe and easy way of identifying first year birds.

Tertials are generally edged paler brown in first year birds than in adults. Due to individual variation, only those birds whose tertials have whitish edges should be aged as 1y by this characteristic alone. On autumn migration, tertials of first year birds are slightly worn at tips (Plates 2-3).

Adults (2y+) only have one generation of feath-

Table 4. Moult patterns in Tree Pipits (N. Europe).

Ruggningsmönster hos trädpiplärka (Nordeuropa).

Summer *sommar*	Winter *vinter*
2y+/2+: Complete after breeding (SC). *Komplett efter häckning (SC).*	**All ages/*alla åldrar*:** Partial (wp): Body-f., some LC, MC and GC, usually all TE and central pair of TF. *Partiell (wp): Kroppsfj., några mindre (LC), mellersta (MC) och större täckare (GC), vanligen alla tertialer (TE) samt centrala paret stjärtpennor (TF).*
1y/*1k*: Partial (sp): Body-f., some (rarely all) LC, sometimes some MC. Rarely 1-3 inner GC. Exceptionally an odd TE and central pair of TF. *Partiell (sp): Kroppsfj., en del (sällan alla) mindre täckare (LC) och ibland även mellersta täckare (MC). Mera sällan 1-3 större täckare (GC). Undantagsvis någon tertial (TE) och centrala paret stjärtpennor (TF).*	

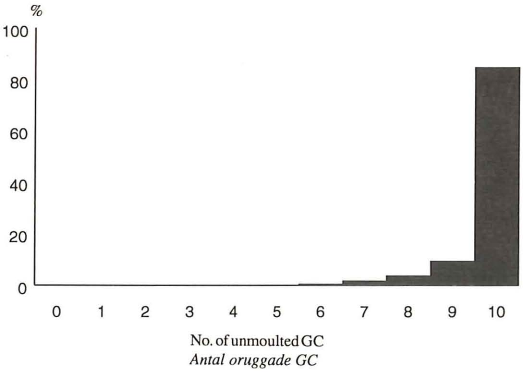


Fig. 1. Percentage unmoulted greater coverts (GC) in first year (1y) Tree Pipits trapped during autumn migration.

Procentuell fördelning av antalet oruggade större täckare (GC) hos unga (1k) trädpiplärkor fångade under höstflyttningen.

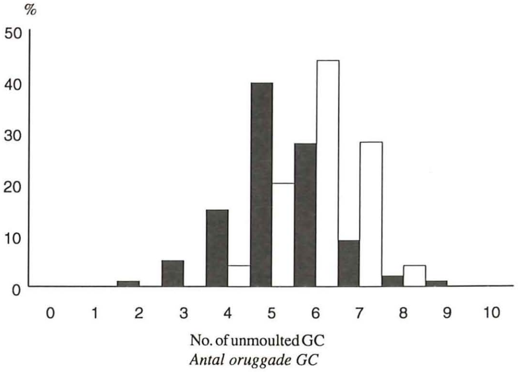


Fig. 2. Percentage unmoulted greater coverts (GC) in Tree Pipits trapped during spring migration.

Procentuell fördelning av antalet oruggade större täckare (GC) hos trädpiplärkor fångade under vårflyttningen.

ers after complete moult, and the whole plumage is fresh (Plates 4-5). In some specimens, secondaries are still growing at the onset of migration (growing feathers shorter than the full-grown ones or sheath-remains still left at the base of inner secondaries, usually SS_4-5). These birds are easily aged as adults by this characteristic alone.

Iris colour is another good and, after some practice, easy way of ageing Tree Pipits in autumn. It is also possible to separate second year birds (2y) from older ones (3y+). At least, birds with iris clear brown are always 3y+ (Plate 8:A-C).

Spring (after wp-moult, up to SC-moult)

Since we have no records of Tree Pipits with all tail-feathers moulted during partial winter moult, the pattern of TF_5 is useful for ageing also in spring (Plate 1:C,F,G). A few birds may be difficult to age due to wear of tail-feathers, and there is a possibility of an odd 2y with all tail-feathers moulted and thus showing the "wrong" pattern.

Partial winter moult includes all ages and thus all birds show moult contrasts among wing-coverts after this moult is finished. This makes ageing by characteristics of the wings difficult. However, unmoulted feathers (PP, SS, PC, unmoulted LC, MC & GC) are generally more worn and bleached in 2y than in older (3y+) birds (Plates 6-7), making the moult contrasts more prominent. The examples shown in Plates 6 and 7 are typical. Due to individual variation in wear there are some ambiguous cases.

Iris colour will help in most cases. Typical 2y only have a very slight brownish tinge, while typical 3y+ are clear brown at least on outer parts and above the pupil (Plate 8:B-C).

Details, comments and statistics

Moult

In first year birds (1y) only 15% (N=594) had moulted any greater coverts (Fig. 1), compared to 27% in migrating Tree Pipits trapped in Switzerland (L. Jenni in Glutz & Bauer 1988), and less than 10% in Israel in October (P. Alström in litt.). If any greater coverts are moulted, GC_9 rather than GC_10 is the first one moulted (Plate 3). Tertials and tail-feathers are normally not moulted (only very rarely an odd tertial or the central pair of tail-feathers).

Complete summer moult (SC) exceptionally leave a few lesser coverts (Plate 5:C) or other single wing-feathers (e.g. the lesser alula feathers; P. Alström in litt.) unmoulted, even one or two secondaries (S_4, S_5) (Riddiford 1990, P. Alström in litt.).

Winter partial moult (wp) includes all ages and we found no significant difference useful for ageing. Unlike the partial summer moult (sp), a number of greater coverts (usually 4-6) are always replaced (Fig. 2), while some birds retain all lesser and median coverts unmoulted. Tertials are often moulted (Table 6) and so is the central pair of tail-feathers, but rarely more (Table 7). When not moulted, the central pair of tail-feathers is very worn in spring (cf. Plate 1:F), sometimes only the shaft is left. On average adults (3y+) seem to moult less and vary less

Table 5. Ageing criteria in Tree Pipits. *Kriterier för åldersbestämning av trädpiplärka.*

All year/*hela året:* autumn – summer, up to SC-moult *höst – sommar, fram till SC-ruggning*	
1y–2y spring/*1k–2k vår*	**2y+ autumn – 3y+ spring/*2+höst – 3+ vår***
White pattern on inner web of TF_5 rather indistrinctly set off ("looks dirty"). Only little white on outer web of TF_5, not fading along the edge (making dark tip rather blunt). *Vitt på innerfan av stjärtpenna 5 (TF_5) ganska otydligt avgränsat ("grötigt"). Det vita på ytterfan av TF_5 avtar ganska tvärt mot kanten och formar en trubbig topp på fjäderns mörka del.* ***1:A-C (G)***	White pattern on inner web of TF_5 quite distinctly set off. White on outer web of TF_5 fading gradually along the edge (making dark tip very pointed). *Vitt på innerfan av stjärtpenna 5 TF_5 ganska väl avgränsat. Det vita på ytterfan av TF_5 avtar långsamt längs kanten och formar en spetsig topp på fjäderns mörka del.* ***1:D-F (G)***
Autumn/*höst:* plumage criteria up to wp-moult *fjäderdräktskaraktärer fram till wp-ruggning*	
1y/*1k*	2y+/*2+*
Moult contrast among LC or MC, more rarely among inner GC. *Ruggningsgräns bland mindre (LC) eller mellersta täckarna (MC), mera sällan bland de inre större täckarna (GC).* ***2:A, 3:A, C***	No moult contrasts among wing-coverts. N.B. **5:D.** *Inga ruggningsgränser. Obs: **5:D.*** ***4:A, C, 5:A, C***
Unmoulted TE edged pale brown or even whitish. Tips slightly worn from Aug. *Oruggade tertialer (TE) blekt brunkantade eller t.o.m. vitaktiga. Toppar lätt slitna från aug.* ***2:B, 3:B***	TE often edged warm brown. Tips completely fresh at least in Aug – early Sep. *Tertialer (TE) oftast varmt brunkantade. Toppar helt fräscha i aug – början av sept.* ***4:B, 5:B***
TF rather blunt. Tips slightly worn from Aug. *Stjärtpennor (TF) ganska trubbiga, topparna lätt slitna från aug.* ***1:A-B***	TF very pointed. Tips completely fresh at least in Aug – early Sept. *Stjärtpennor (TF) spetsiga. Topparna helt fräscha i aug – början av sept.* ***1:D-E***
Iris uniformly blackish grey. *Iris enfärgat mörkt skiffergrå.* ***8:A***	Iris variously brownish. Clearly brown always 3y+. *Iris med inslag av brun ton. Tydligt brun alltid 3+.* ***8:B-C***
Spring/*vår:* plumage criteria up to SC-moult *fjäderdräktskaraktärer fram till SC-ruggning*	
2y/*2k*	3y+/*3+*
Unmoulted wing coverts and tips of PP normally rather heavily worn. *Oruggade vingtäckare och topparna på handpennorna (PP) normalt ganska kraftigt slitna och blekta.* ***6:A-D***	Unmoulted wing coverts and tips of PP normally only slightly worn. *Oruggade vingtäckare och topparna på handpenna (PP) normalt endast lätt slitna.* ***7:A-D***
Iris still dark slate-grey but with a dull brownish tinge. *Iris fortfarande mörkt skiffergrå men med en svag brun ton.* ***8:B***	Iris variously brownish. Clearly brown always 3y+. *Iris bruntonad. Tydligt bruna alltid 3+.* ***8:C***

Table 6. Number of moulted tertials (TE) in Tree Pipits trapped during spring migration.

Antal ruggade tertialer (TE) hos trädpiplärkor fångade under vårflyttningen.

Age *Ålder*	N	No. of moulted TE *Antal ruggade TE*			
		0	1	2	3
2y *2k*	29	1	0	4	24
3y+ *3+*	24	1	0	1	22

than younger (2y) birds. The extent of the partial winter moult is also individually variable, probably due to the conditions in the winter quarters of individual birds.

Ageing

In autumn, 175 birds were checked for pattern on the second outermost tail-feather (TF_5) compared to other ageing criteria and 96% were correctly aged according to the tail feather criterion.

The same pattern as described for TF_5 can sometimes be seen also on TF_4, though white parts are much smaller (mostly in adults) or absent (mostly in first year birds) (cf. Svensson 1992).

Unlike in most passerine species, tail-feathers in adult Tree Pipits (autumn) are generally somewhat more pointed than in first year birds. Bub (1981) and Busse (1984) assert the contrary for which we have found no evidence.

Adults with a few lesser coverts or other single feathers not included in the complete moult (SC) show a moult contrast among these feathers in autumn. However, the unmoulted feathers in adults are always few, considerably more worn and bleached brown, and cannot be confused with corresponding juvenile feathers (cf. Plates 2:A, 5:D).

In some adults (autumn), the tips of the inner greater coverts are darker than the tips of the rest of the greater coverts. This may look like a moult contrast and age the bird as a 1y. However, the colour of the *edges* of all greater coverts is the same, which is not the case in first year birds with a moult contrast (cf. Plates 3:C and 5:C).

Though not as pronounced as in spring, the shape and structure of primary coverts is a supporting characteristic also in autumn: 1y have their primary coverts rather pointed with a "loose" structure while adults have these feathers more rounded and with a "firm" structure.

Table 7. Number of moulted tail-feathers (TF) in Tree Pipits trapped during spring migration.

Antal ruggade stjärtpennor (TF) hos trädpiplärkor fångade under vårflyttningen.

Age *Ålder*	N	No. of moulted TF *Antal ruggade TF*								
		0	1	2	3	4	5	6	7	≥8
2y *2k*	30	3	1	17	2	5	1	0	1	0
3y+ *3+*	13	2	0	11	0	0	0	0	0	0

Iris colour of 1y is very constant, and could be defined as blackish natural grey (Smithe 1975), when seen in normal daylight or in the light from a daylight fluorescent tube. When seen in morning or evening sunlight or in the light from an ordinary light bulb, the red light of the sun or light bulb will reflect in the iris, and thereby the colour may seem somewhat more dusky brown (Smithe 1975). However, under these circumstances, the browner iris colour of 2y and 3y+ will be coexstensively displaced. Thorough knowledge of this can only be obtained from personal experience.

Acknowledgements

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Report No. 157 from Falsterbo Bird Observatory.

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Sammanfattning

Åldersbestämning av trädpiplärka Anthus trivialis

Kriterier för åldersbestämning av trädpiplärkor *Anthus t. trivialis* visas på färgfoton av levande fåglar. Vinge, stjärt och huvud fotograferades under konstanta förhållanden på 90 trädpiplärkor (Tabell 1). På dessa såväl som på fåglar som inte fotograferades insamlades uppgifter om biometri, ruggningsmönster m.m. Totalt har över 2000 trädpiplärkor hanterats under den tid datainsamlingen har pågått.

För att minska textmassan används förkortningar för ålder (Tabell 2), återkommande benämningar på ruggningsmönster och vissa fjädergrupper (Tabell 3). Förkortningarna är i huvudsak desamma som används av Svensson (1992). För de svenska ålderskoderna har vi valt de äldre beteckningarna 1k, 2k osv. i stället för 10 (ett-noll), 20 osv. Detta för att undvika förväxling med talen 10 (tio), 20 osv. All numrering av fjädergrupper är ascendent (börjar utifrån), utom för stjärtpennorna som räknas från mitten och utåt (1-6).

Ruggning

Trädpiplärkor ruggar två gånger om året (Ginn & Melville 1983): Gamla fåglar (2+) ruggar komplett (SC) på sommaren efter häckningen. Ungfåglarna (1k) ruggar partiellt (sp) vid samma tid. I vinterkvarteren genomgår alla en partiell ruggning (wp). Ruggningsmönstren sammanfattas i Tabell 4. Hand- och armpennor, handtäckare och de flesta stjärtpennor ruggas bara en gång om året (efter häckning). Det innebär att ålderskaraktärer baserade på dessa fjädergrupper är giltiga året om (höst - sommar), medan andra endast gäller under hösten eller vår/sommar.

Det skall påpekas att de ruggningsmönster vi redovisar i Tabell 4 helt och hållet bygger på fåglar fångade i Falsterbo. Andra populationer kan alltså ha något annorlunda omfattning av de partiella ruggningarna (sp, wp).

Åldersbestämning i huvuddrag

Kriterier för åldersbestämning listas i Tabell 5 och visas på bilderna 1-8. Använda i kombination möjliggör dessa kriterier korrekt åldersbestämning under hela året.

En urmakarlupp med ca 5 gångers förstoring är ett utmärkt (och nödvändigt) hjälpmedel vid fjäderstudier. Vid studium av irisfärg behövs ca 10 gångers förstoring och goda ljusförhållanden.

Höst (efter SC/sp-ruggning, fram till wp-ruggning)

Skillnaden i mönster på näst yttersta stjärtpennan (TF_5; Bild 1) är lättast att se på hösten då stjärtpennorna är fräscha. Ungfåglar (1k) har mindre tydlig gräns mellan vitt och brunsvart på innerfan samt mindre vitt på ytterfan av TF_5 än gamla (2+) fåglar. De mörka partierna går ut i en sylvass spets hos 2+. Utbredningen av vitt på innerfan av TF_5 verkar inte vara bundet till fågelns ålder.

Topparna på de yttre stjärtpennorna är lätt slitna hos ungfåglarna redan från mitten av augusti medan de gamla fåglarna då har dessa fjädrar helt fräscha. Eventuell förslitning syns väl om man håller stjärtpennorna upp mot en lampa eller mot himlen (Bild 1: A-B, D-E).

Efter den partiella sommarruggningen har ungfåglarna alltid två generationer vingtäckare. Ruggningsgräns förekommer oftast bland de mindre täckarna, ovanligare bland de mellersta och mera sällan bland de större täckarna (Bild 2-3). Detta är en lätt och säker metod för åldersbestämning på hösten.

Hos ungfåglarna är tertialerna oftast blekt ljusbruna längs kanterna medan de hos de gamla fåglarna är varmt bruna. Viss individuell variation förekommer, och endast fåglar vars tertialer har vitaktiga kanter bör bestämmas till 1k på enbart denna karaktär. Under höstflyttningen är topparna på tertialerna lätt slitna hos 1k (Bild 2-3).

Gamla (2+) fåglar har endast en generation fjädrar efter avslutad ruggning (SC) och fjäderdräkten är hel och fräsch. Vissa exemplar kan lätt åldersbestämmas på att de inre armpennorna (SS_4-5) inte är fullt utväxta eller att de har spolrester kvar vid basen.

Irisfärgen är ett annat säkert och (efter träning) enkelt kriterium för åldersbestämning, eftersom alla

1k har samma irisfärg utan spår av brunt (Bild 8:A). Det är också möjligt att bland de gamla fåglarna skilja ut 2k och 3+ (Bild 8:B-C), åtminstone är fåglar med tydligt brun iris alltid 3+.

Vår (efter wp-ruggning fram till SC-ruggning)

Eftersom trädpiplärkor endast i yttersta undantagsfall ruggar alla stjärtpennor på vintern, är mönstret på TF_5 användbart för åldersbestämning även under våren (Bild 1:C,F,G).

Den partiella ruggningen i vinterkvarteren omfattar alla åldersgrupper. Därför har såväl 2k som 3+ ruggningsgränser på vingarna om våren. Generellt är de oruggade fjädrarna (PP, SS, PC samt oruggade LC, MC och GC) mer slitna och blekta hos 2k än hos 3+ (Bild 6-7), vilket gör att ruggningsgränserna framstår tydligare hos 2k. Bild 6-7 visar typexempel. På grund av individuell variation i slitaget av fjädrarna förekommer mera svårbestämda exemplar.

Irisfärgen är ett hjälpmedel även under våren (Bild 8:B-C). 2k har (som mest) en svag brunton, medan 3+ är mera tydligt bruntonade, särskilt i yttre delen av iris och ovanför pupillen.

Detaljer, kommentarer och statistik

Ruggning

Endast 15% av 594 undersökta 1k hade ruggat någon större täckare (GC) (Fig. 1), vilket kan jämföras med 27% i en schweizisk undersökning (L. Jenni i Glutz & Bauer 1988), och mindre än 10 % i Israel (P. Alström i brev). I allmänhet verkar GC_9 ruggas före GC_10 (Bild 3). Tertialer och stjärtpennor ruggas bara i undantagsfall och då någon enstaka fjäder.

Sällsynt kan 2+ ha enstaka oruggade vingfjädrar kvar efter den kompletta sommarruggningen. Ofta är det någon mindre täckare (Bild 5:C), men även någon alulafjäder eller någon armpenna kan lämnas oruggad (Riddiford 1990, P. Alström i brev).

Vinterruggningen (wp) omfattar alltid ett antal större täckare (vanligen 4-6, se Fig. 2), medan vissa fåglar lämnar alla mindre och mellersta täckare oruggade. Tertialerna ruggas ofta (Tabell 6), likaså centrala paret stjärtpennor, men sällan fler (Tabell 7). Oruggade centrala stjärtpennor är mycket slitna på våren (Bild 1:F), ibland återstår bara skaftet av fjädern.

2k verkar i genomsnitt rugga något mer än 3+ och dessutom variera mer. Den individuella variationen, antagligen beroende på förhållandena på övervintringslokalen, är emellertid också stor.

Åldersbestämning

175 fåglar åldersbestämdes efter mönstret på näst yttersta stjärtpennan (TF_5) och jämfördes därefter med andra ålderskriterier under hösten. 96% blev rätt åldersbestämda efter stjärtpennemönstret.

Samma mönster som på TF_5 finns ibland även på TF_4, men är mindre utbrett (jfr. Svensson 1992). Till skillnad från de flesta tättingarter har 2+ (höst) trädpiplärkor i allmänhet spetsigare stjärtpennor än 1k.

Hos en del 2+ (höst) har de inre större täckarna något mörkare toppar än övriga. Detta kan förväxlas med en ruggningsgräns, men ytterkanterna av samtliga större täckare har samma färg hos 2+, vilket inte är fallet hos en 1k med ruggningsgräns (jfr. Bild 3:C och 5:C).

Trots att skillnaderna inte är så tydliga som på våren kan form och struktur hos handtäckarna vara till hjälp vid åldersbestämning även på hösten. 1k har ganska spetsiga handtäckare med "lös struktur", medan 2+ har mera rundade med "fast" struktur och kontur.

Irisfärgen hos ungfåglarna är mycket enhetlig och kan definieras som "blackish natural grey" (Smithe 1975). Ljuset från omgivningen kan dock reflekteras i iris så att den i t.ex. morgon- eller aftonsol ser ut att ha en brun nyans ("dusky brown" Smithe 1975). Under sådana omständigheter förändras naturligtvis också den brunare irisfärgen hos 2k och 3+ i motsvarande grad.

Meddelande nr 157 från Falsterbo fågelstation.

Short Communications Korta rapporter

Responses of nesting Meadow Pipits *Anthus pratensis* and White Wagtails *Motacilla alba* to a stuffed Sparrowhawk *Accipiter nisus*

FRANK GÖTMARK

Abstract. I examined responses of nesting Meadow Pipits and White Wagtails to a mounted Sparrowhawk. The birds flew to and circled above the predator, apparently to inspect it, and then landed some distance away. Both species approached the predator, but wagtails approached it closer during "inspection" flights and landed much closer to it after flights than did pipits. The birds may inspect the predator to obtain useful information; the difference between species may be related to flight capacity and nesting habitat.

Much is known about the reproductive behaviour of birds, but other aspects of their behaviour remain largely unexplored. Anti-predator behaviour is such an aspect; a check in a handbook such as *Birds of the Western Palearctic* reveals that in many species surprisingly little is know about how individuals respond to and avoid predators. This applies especially to predators of adults and juveniles, such as *Accipiter* hawks, which are difficult to detect and observe for ornithologists in woodland. Stuffed specimens of predators (e.g. owls and raptors) have been used to study responses and mobbing behaviour in passerines (e.g. Curio 1975, Curio et al. 1983, Alatalo & Helle 1990). Responses seem to depend on the species of predator (the danger it poses) and the distance to the prey. However, to date only a few common passerines have been studied.

In this study I examined responses of two quite closely related passerines, the Meadow Pipit *Anthus pratensis* and the White Wagtail *Motacilla alba* (Cramp 1988), to a stuffed, perched Sparrowhawk *A. nisus*. An earlier study suggested that Sparrowhawks show no preference for any of these two prey species: in paired trials, mounted pipits were attacked as often as mounted wagtails. Further analysis indicated that the plumage of the two species may be about equally conspicuous, as judged from the appearance of mounted specimens in the wild (Götmark, *submitted*). However, the two species seem to differ in anti-predator behaviour: the wagtail is known to mob flying hawks with a special mobbing-song, a behaviour which has not been recorded in the pipit (Bergmann & Helb 1982, Cramp 1988). To study their behaviour in more detail, I compared responses to a stuffed Sparrowhawk placed in nesting territories of the two species.

I conducted the study in April and May 1991 near Göteborg. Meadow Pipits were studied at a bog (Rambo mosse) 2 km southwest of Mölnlycke, and on grazed meadows 1 km southeast of Kungälv. I studied wagtails at lakes, streams, and near human habitation in the same area. Experiments were performed before or during egg laying (a few pairs may have had started incubation). The stuffed Sparrowhawk (a juvenile female) was mounted on a 1 m-pole that was pressed down into the ground. I used singing or displaying males or birds giving alarm calls as indications of a nesting territory. The mounted Sparrowhawk, covered with a grey plastic bag, was placed in what seemed to be the centre of the territory (singing and neighbouring males were observed briefly before each experiment). Only one experiment was conducted in each territory. I monitored each territory from a hide about 30 m from the mount, and started observations when the birds showed normal, undisturbed behaviour or when I could no longer hear any alarm calls. The wagtails were then usually visible on the ground some distance from the mount, while it was more difficult to watch pipits in the higher grass or herb vegetation that characterizes their nesting territories. With the mount hidden in the bag I first recorded the behaviour of (visible) territory owners during 10 min. Then, with the aid of a string, I pulled the bag off the hawk, and recorded responses to the mount during at least 10 min.

No bird showed a response to the pole or mount covered by bag, suggesting that these artifacts did not influence the behaviour of the prey species. A few birds were recorded passing the bag in flight without noticing it. No bird was closer than 15 m from the mount. When the bag was pulled off the mount, the wagtails and pipits soon detected it, but wagtails detected it earlier (mean = 3.8 min ± 2.2 (SD), n = 10 experiments) than pipits (10.1 ± 9.8, n = 11 experiments; P = 0.04, Mann -Whitney U-test, two-tailed). Both species responded in a similar manner after they had detected the mount. They flew to it and circled it several times for about a minute, then they landed on the ground or in low bushes some distance away, watching the mount for some time. The birds sometimes called as they flew over the mount.

However, in flight wagtails approached the mount closer than did pipits. The closest distance to the mount during "inspection" flights was on average 3.1 m (±2.1) for wagtails and 10.1 m (±8.4) for pipits (P=0.002). Moreover, the average landing distance from the mount after inspection flights was much shorter for wagtails (8.9±11 m) than for pipits (57±29 m; P=0.0005). This was probably not due to differences in territory size, since wagtail territories appeared to be larger than those of pipits (Götmark, pers. obs.)

Thus, both species clearly approached the predator, since no bird visited the site of the mount pole when the mount was covered. Why do these passerines approach a potentially dangerous predator so closely? One possible or likely reason is that prey species are selected to seek information about predators (Kruuk 1976, Curio 1978). Information about appearance, behaviour, and intentions of predators might be useful for prey, as they throughout their life need to avoid them in critical situations (in an evolutionary perspective, also humans are prey and are attracted to danger and violence, such as in films and in the media). Once a bird (prey) has detected a hawk, it is unlikely to be caught, as hawks are usually only able to catch prey that are unaware of the predator. Therefore the risk taken by wagtails and pipits during inspection flights might be relatively small. However, there are alternative explanations of the observed behaviours. I interpret them as a form of predator "inspection", but according to the definition of Curio (1978) the prey species are "mobbing" the predator, and then there are at least six alternative explanations for their behaviours (see Curio 1978).

Sparrowhawks seem to regard White Wagtails and Meadow Pipits as equally profitable prey (Götmark, *submitted*). Given a clear risk of predation, why do flying wagtails approach a stuffed hawk more closely than do pipits (in addition, wagtails also mob flying hawks; Bergman & Helb 1982)? They do not seem to be more manouvrable in flight than pipits, because a comparison of wing loading (wing area divided by weight; a low wing loading implies improved manouvrability in flight) in the two species showed no significant difference (Götmark, *submitted*). However, wing loading is only one aspect of flight capacity, and the species may differ in, for instance, maximal flight speed. Wagtails occur in habitats devoid of or with only low vegetation, where visibility is good, whereas pipits occur in grassland with higher ground vegetation. Given that visibility is good, wagtails may detect approaching hawks early. The pipit, on the other hand, may have been selected to seek cover far away from a predator, as lower visibility makes it difficult to watch the predator continously or detect a predator early. This interpretation is consistent with the earlier detection of the hawk mount in wagtails than in pipits. However, it does not explain why wagtails flew closer to the predator during inspection flights. Possibly, this difference reflects superior flight capacity in the wagtail.

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Sammanfattning

Häckande ängspiplärkors och sädesärlors reaktioner på en uppstoppad sparvhök

Fåglars reaktioner inför predatorer, såsom rovfåglar, är bristfälligt kända. Hos vanliga arter (t ex talgoxe och svartvit flugsnappare) har man studerat så kallat mobbningsbeteende, där bytesarterna närmar sig, exponerar sig, och på olika sätt markerar sitt "missnöje" för predatorn. Reaktioner inför viktiga predatorer som sparvhök och duvhök är dock okända hos många av våra mindre vanliga tättingar.

I denna studie undersökte jag hur häckande sädesärlor och ängspiplärkor reagerade inför en uppstoppad sittande sparvhök som placerats i deras revir. Då denna var täckt reagerade inte fåglarna (inför sittpinne och min närvaro). Då höken exponerades flög de mot höken, flög runt över den någon minut, och avlägsnade sig därefter. Sädesärlorna upptäckte höken tidigare, flög runt på kortare avstånd från höken, och landade avsevärt närmare höken än ängspiplärkorna.

Jag tolkar båda arternas beteende som en form av inspektion av predatorn, genom vilken de kan informera sig om dess beteende och avsikter. Då de redan upptäckt predatorn löper de liten risk att attackeras av den, eftersom hökar normalt bara fångar byten som ännu inte upptäckt deras närvaro. Det finns emellertid alternativa förklaringar till bytesarternas beteende om man klassificerar det som "mobbning" (se Curio 1978).

Skillnaden mellan arterna kan delvis bero på olikartat habitatval; ängspiplärkor föredrar miljöer med högre vegetation än sädesärlor. För ängspiplärkor innebär detta att det kan vara svårare att upptäcka eller bevaka en predator i närheten och det kan därför vara fördelaktigt att landa långt ifrån den. En alternativ förklaring till sädesärlornas mer "oskygga" beteende kan vara att de är bättre på att undkomma sparvhökar (t ex genom bättre flygförmåga).

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Gustaf fyller åttio

Den 30 oktober 1993 fyller Gustaf Rudebeck åttio år! En levande legend inom svensk ornitologi. För många har han varit en läromästare. Många har blivit inspirerade av honom. Fler kommer att bli det, Gustaf är fortfarande aktiv!

Naturligtvis måste han hyllas alldeles extra på födelsedagen. Här är Din chans att gratulera Gustaf genom att skänka pengar till en fond. Samtidigt gör Du en insats för fåglarna och ornitologin i Gustafs anda.

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John M. Marzluff & Russell P. Balda: **The Pinyon Jay.** Illustrerad av Tony Angell. 317 sid. T. & A. D. Poyser, London. Medlemspris i Naturbokhandeln, inb.: 253 kr. ISBN 0-85661-064-X.

Den här boken handlar om en fågelart, pinjeskrikan *Gymnorhinus cyanocephalus,* som verkar ha nästan allting. Vad jag menar med detta kommer att framgå om man läser boken och kanske även litet genom denna bokanmälan. Materialet bygger på en långtidsstudie av arten (fältarbetet inleddes 1968) som alltjämt fortgår. Pinjeskrikan förekommer i sydvästra U.S.A., där den är starkt knuten till pinjetallen *Pinus edulis* och ponderosatallen *P. ponderosa,* och kan väl betraktas som en ekologisk motsvarighet i Nordamerika till vår smalnäbbade nötkråka *Nucifraga caryocatactes macrorhynchus,* som lever på cembratallens *P. cembra* frön.

Författarna förmedlar genom hela boken känslan att den här arten har *det*, en kombination av skönhet och gåtfullhet. Efter att ha läst boken och tagit del av alla fakta har dock det mesta av denna gåtfullhet reducerats till ett minimum. Men man är böjd att hålla med om att pinjeskrikan är ett mycket intressant studieobjekt. Den lever som sagt huvudsakligen på pinjetallens frön, vilkas talrikhet varierar enormt mellan åren. Därför tvingas fåglarna ibland ut på flyttning för att söka upp nya områden med tillgång på föda. Detta avspeglas morfologiskt i relativt långa vingar – en anpassning för effektiv flygning. Frönas säsongsmässiga tillgång har även medfört att pinjeskrikan hamstrar nötter för senare användning. Även under hamstringsperioden flyger fåglarna mycket och har då nytta av sina långa vingar. För att transportera upp till 40-50 frön har fåglarna utrustats med en extra tänjbar matstrupe som därför fungerar utmärkt som transportpåse. Arten är monogam och häckar i kolonier på omkring 100 individer. Huruvida fåglarna är strikt monogama hoppas jag forskarna tänker undersöka vidare med moderna molekylärbiologiska metoder som nu finns att tillgå. Dessutom förekommer ett "hjälparsystem", dvs vissa individer häckar inte själva utan hjälper istället ett par med häckningen.

Boken behandlar utförligt artens biologi i 13 kapitel, som bl.a. tar upp systematik, samevolution med pinjetallen, läteskommunikation, demografi, partnerval, häckningsbiologi, dispersion och mortalitet. Den avslutas med sex appendix där mycket av basdata presenteras. Informationsmängden är imponerande och den baseras på gediget fältarbete och många studenters outtröttliga observationer. Resultaten diskuteras i relation till modern ekologisk teoribildning. På grund av att studien inleddes så tidigt som 1968 har teoriutvecklingen gjort stora framsteg under studiens gång. Det är möjligen här bokens största svaghet finns på grund av att det äldre materialet sällan lämpar sig till att effektivt testa nyare hypoteser. Detta är normalt eftersom datainsamling måste skräddarsys för en given hypotes man önskar belysa. Därför blir diskussionerna ofta spekulativa och läsaren lämnas ofta med frågan obesvarad. Detta är emellertid ingen större nackdel jämfört med det stora värdet studien har just därför att den pågått så länge.

Ett mycket intressant avsnitt behandlar frågan om varför det förekommer hjälpare, i det här fallet yngre hanar som hjälper sina föräldrar att föda upp flera syskon. Den gängse förklaringen grundar sig på sk släktskapsselektion. Istället för att, som relativt oerfaren ungfågel, så gott som säkert misslyckas med en egen häckning lönar det sig bättre att hjälpa föräldrarna att föda upp besläktade individer, t ex syskon. På så sätt lyckas hjälparen i viss utsträckning föra sina gener vidare till nästa generation. Hos pinjeskrikan observerade man dock att hjälparna inte alls medförde någon förbättrad häckningsframgång för föräldrarna jämfört med om de var utan hjälpare. Istället är det så att föräldrarna hjälper den unge hanen genom att låta honom stanna kvar i reviret ytterligare en häckningssäsong. På så sätt får ungfågeln en bättre start i livet och behöver inte ansluta sig till ungfågelflocken där det är mycket hård konkurrens. Det var bara de bästa paren som hade råd att hjälpa sina ungdomar på detta sätt.

Sammantaget är det här en mycket intressant bok, som innehåller mycket fakta om en spännande fågelart och som förmedlar den fascination forskarna känner inför sitt studieobjekt.

MATS GRAHN

A. Lundberg & R. Alatalo: **The Pied Flycatcher.** T. & A. D. Poyser, London. 267 sid. Medlemspris i Naturbokhandeln: 243 kr. ISBN 0-85661-072-0.

If someone decided to write a book on controversies in behavioural ecology, he or she could not avoid picking examples from the pied flycatcher. Since Arne Lundberg and Rauno Alatalo (L & A) and their colleagues in Uppsala published their first papers in 1981 there has been a lively debate over several aspects of the breeding system of this fascinating species. The case of the pied flycatcher is an excellent example of how an innovative research programme can stimulate critical thinking and hypothesis testing by other research groups and how such interaction between groups leads to a rapid evolution of ideas and better understanding of biological problems. Personally, I think that many fields of biology would benefit from becoming more "competitive", and researchers should become far more dedicated to testing each others results.

The pied flycatcher has become one of the core species of behavioural ecology. It is hard to find any textbook in this field that does not have a list of references to publications by L & A. I have often admired their elegant experiments and their clear writing, though I must say I often have disagreed with their interpretations. Readers are hereby warned; this review is written by one of L & A's critics! But before I express my criticism let me explain briefly what the book is about.

L & A's book is a comprehensive review of the natural history, the life history, the ecology and the behaviour of the pied flycatcher. Some new information is included, especially from their English study site. However, on the whole the book is a synthesis of previously published work. In light of the huge file of publications on this species (more than 300 papers are cited in the book), L & A have been successful in extracting the most important information. The chapters span topics like taxonomy, hybridization, migration, foraging and reproduction, and thus cover much more than the actual research areas of L & A. No doubt, through this book amateur ornithologists have easy access to an important part of the scientific literature. Even to the professional the book will serve a valuable digestive function. In particular, I liked the section about nomenclature, which gives a good lesson of the rules, and often complex history, of how species get their scientific names. Such information is seldom seen in the ornithological literature. Also, I must express my admiration for the delicate drawings by Tomas Pärt.

So then, is this book about controversies in the pied flycatcher literature? To those who hoped it was, the book must be a disappointment. The controversial issues are there, but L & A ride their same old horses. Given the monograph-like character of the book one might expect a deeper and more balanced analysis of alternative ideas. To those who are not familiar with these controversies, or do not discover them when reading the book, let me deal specifically with a few. I start with the most famous controversy, namely that of explaining polyterritorial polygyny.

Many pied flycatcher males are bigamous, having their two females in widely separated territories. The secondary female apparently pays a cost of polygyny because she receives less assistance from the male in raising her offspring than does a female that mates monogamously. Hence, there are two questions that must be answered before the evolution of polyterritorial polygyny can be fully understood. First, why do males defend widely separated territories? And second, why do females mate with already mated males? L & A have proposed the *Deception* hypothesis that gives an answer to both hypotheses at the same time: polyterritorial behaviour enables the male to hide the fact that he is already mated, and hence improves his mating success. Consequently, the secondary female is deceived into polygyny. This view emphasizes an active and deceptive role of the male. The alternative ideas, advocated by the "Oslo" group, focus on the active role of females. First, the *Female Aggression* hypothesis states that a mated female will try to prevent her mate from getting a second mate, because polygyny is also costly to the primary female. Therefore, the male tries to reduce the effect of aggression from his first mate by taking up a distant territory. Hence, the Female Aggression hypothesis explains just why males are polyterritorial. To explain why females mate with already mated males, the "Oslo" group has launched the *Search Cost* hypothesis. This idea assumes that females are fully able to discriminate between unmated and already mated males, but that they accept secondary mate status because it is too costly to keep on searching for an unmated male.

The most important cost is the risk of losing the breeding opportunity to another prospecting female, with the possible consequence of not finding any other opportunity. This hypothesis is consistent with the common belief that many pied flycatchers, even females, are prevented from breeding because of a lack of suitable nest holes. It also explains why females have a very restricted mate search; they generally visit only a few males before making their choice.

L & A fail to make a fair presentation of these alternative hypotheses. They do not discriminate between the above questions as two independent problems of polyterritoriality and polygyny. Under the section *"Why are pied flycatcher males polyterritorial?"* they contrast the Deception and the Search Cost hypotheses, despite the fact that the latter has never been intended to explain why males are polyterritorial. L & A state explicitly (page 210) that *"The third point [for doubting the search cost hypothesis] is that the search cost hypothesis cannot explain why males are polyterritorial"*. Then they make a comment about the Female Aggression hypothesis as if it were formulated as a desperate attempt to save the remnants of the Search Cost hypothesis. They finally try to strangle the Female Aggression hypothesis the same way as with the Search Cost hypothesis by stating that the Female Aggression hypothesis is *"not a sufficient explanation for the poor choices made by the secondary females"*. Their statement is irrelevant because the Female Aggression hypothesis is about polyterritoriality and not about the mate choice of secondary females. L & A seem to think that the Deception hypothesis is superior to all others because as they say (on page 211): *"Our major objection, however, to all these other hypotheses is that they cannot explain both why secondary females should accept a situation leading to reduced reproductive success and why males are polyterritorial; at most they can explain one or the other"*. I cannot buy such an argument, neither should any reader, because there may be several factors producing a given mating system, and one hypothesis should not have to explain every facet.

There are two other controversies that I would like to mention more briefly. One is the reason why males have a variable plumage colour, ranging from brown to black. The problem is to identify any advantage to males from being black. Despite the fact that several Norwegian studies have reported that black males are preferred by females more than brown males, L & A refuse to accept that blackness is selected through a female choice mechanism. They do not mention that after a nesting failure females are more likely to divorce brown than black males. Instead, they interpret their own evidence for a mating advantage of black males as resulting from male-male competition. Although I can agree that there are general problems in separating the two mechanisms of sexual selection in studies like these, it is puzzling why L & A consistently display resistance against accepting any ability of females to pick out good mates.

The last controversy relates to the intensity of sperm competition. L & A argue that polyterritorial males face a trade-off between guarding their fertile mate and advertizing for a second female. Swedish pied flycatcher males leave their primary female around start of egg-laying, and, as a consequence, risk losing paternity to neighbouring males that might copulate with the female in their absence. In support of this claim is the finding that approximately 18% of all nestlings are fathered by extra-pair males. In contrast, a Norwegian study reported a much lower proportion of extra-pair offspring, i.e. only 4%, even though males left their mates unguarded several days prior to start off egg-laying. Ignoring any controversy over these estimates for this time, the point I want to make here is that while A & L assume a paternity cost to male polyterritoriality, the alternative view is that such a trade-off does not exist, but the latter is not mentioned in the book. This controversy is again a reflection of different emphasis over the role of the two sexes in shaping the mating system. While L & A regard the female as more or less a passive object for copulatory competition among males, the alternative explanation is that female pied flycatchers actively avoid being inseminated by extra-pair males. Hence, there may not be any need for males to guard their mates.

Taken together, these examples reflect a consistent tendency of A & L to regard aspects of the mating system of the pied flycatcher solely from the male perspective, and to ignore any adaptive roles for females: 1) males are polyterritorial in order to deceive females rather than reducing the cost of primary female aggression, 2) secondary females make a maladaptive, not an adaptive mate choiche, 3) male-male competition is more influential than female choice in determining male mating success, and 4) sperm competition is under male and not female control.

It is tempting to put this book in an historical perspective. Ever since Darwin has the role of females been a matter of controversy in sexual selection theory. However, after many debates an initially male-biased approach is being replaced by a more balanced view that allows an adaptive role for females. Female choice has definitely become a recognized mechanism of sexual selection. Female choice models also form the modern basis for categorizing and understanding avian mating systems. At present, we are witnessing a shift in sperm competition theory toward a much stronger emphasis on the role of females in influencing the intensity and outcome of sperm competition. With this background, it seems that many of the controversial ideas put forward by L & A have been a product of a particular way of thinking in the past two decades. If I am correct, such ideas may not survive the nineties.

My conclusion is that in most respects this book is a wellwritten review of existing pied flycatcher literature. As such it will be valuable to many amateur ornithologists and others unfamiliar with the scientific literature. On the other hand, as a scientific contribution itself it has a lower value. The book may however have one unintended and thought-provoking message to the scientific community. Researchers studying the same problem may come up with totally different answers, not so much because of the often stochastic nature of biological patterns, but rather because of different modes of interpretation. Hence, the only basic truth of biology is that any truth is a Red Queen.

JAN T. LIFJELD

Monk, J. F. (red.): **Avian Systematics and Taxonomy.** Bulletin of the British Ornithologists' Club, Centenary volume (Volume 112A). 300 sidor, British Ornithologists' Club, Dorchester 1992. Pris 35 pund.

British Ornithologists' Club bildades 1892, närmast väl som en förening för inbördes beundran för den tidens mera kända engelska ornitologer. Ernst Mayr som i sin ungdom kände mellankrigstidens koryféer i BOC berättar f ö i bokens förord en anekdot som visar att deras inbördes relationer dock inte alltid var helt harmoniska. Under en BOC-middag hade man framskridit till den punkt då cigarrerna skickades runt. Överste Meinertzhagen räckte då cigarrlådan (med tre-fyra cigarrer kvar) till Jourdain ((ö)känd äggsamlare) med kommentaren "ta hela kullen du, som du brukar".

Föreningens tidskrift var från början i stor utsträckning inriktad på publicering av godbitarna i medlemmarnas samlingar och kan väl i viss utsträckning fortfarande sägas vara kvar i samma "nisch". I nutiden är det främst faunistik från olika exotiska områden och systematik som fyller tidskriften. I synnerhet publiceras en häpnadsväckande stor del av alla beskrivningar av nya fågeltaxa i "Bull. BOC".

Det är alltså mycket passande att den jubileumsvolym som utkom till BOC:s hundraårsjubileum 1992 handlar om fåglarnas taxonomi och systematik och man kan konstatera att man har lyckats få anmärkningsvärt många av "de stora kanonerna" inom området att medverka.

Som vanligt i volymer av denna typ är kvaliteten på innehållet ojämn. I synnerhet faller C. H. Fry's artikel om myrmekofagi hos afrikanska fåglar ganska rejält utanför bokens tema även om den i och för sig inte är ointressant. Den av de ingående artiklarna som kommer att bli mest rådfrågad är utan tvivel Vuilleumier's, LeCroy's och Mayr's översikt och värdering av nya fågelarter beskrivna 1981-90, den senaste i en serie från AMNH (och Ernst Mayr) som pågått sedan 1938! Ett klart sammanhang med denna artikel har ett annat bidrag från LeCroy och Vuilleumier som handlar om hur en beskrivning av en ny art *bör* se ut och publiceras. Vid en jämförelse av de båda artiklarna kan man tyvärr konstatera att skillnaderna mellan ideal och verklighet ofta är mycket stora.

Andra bidrag som förtjänar att nämnas särskilt är en artikel av Jürgen Haffer där han med sedvanlig tysk grundlighet utreder artbegreppets historia inom ornitologin, en mycket intressant artikel av Clancey om bakgrunden till underarter, kliner och kontaktzoner i södra Afrika och en motsvarande analys för västafrikanska regnskogsfåglar av Louette. Den sistnämnda artikeln inbjuder osökt till jämförelser med Haffer's klassiska *Avian spectation in South America,* och man slås då av att de biogeografiska mönstren är mycket enklare och diversiteten är mycket mindre bland regnskogsfåglar i Afrika än i Sydamerika, något som säkert går tillbaka på historiska orsaker.

En uppsats som klart avviker från de övriga är en beskrivning av NHM:s (Natural History Museums) fågelsamling av Knox och Walters, en redogörelse som med fördel kan konsulteras i förväg av alla som har ärende till samlingarna i Tring.

Sammanfattningsvis så är detta en bok som är väl värd att skaffa för den som intresserar sig för fågelsystematik, även om priset får anses vara ganska högt relaterat till bokens omfång.

TOMMY TYRBERG

Nya doktorsavhandlingar *New dissertations*

Redaktör ***Editor:*** **S. Åkesson**

Kjell Larsson, 1992: **Ecological and quantitative genetic processes in a population of the barnacle goose (*Branta leucopsis*).** Filosofie doktorsavhandling, Zoologiska institutionen, Uppsala Universitet. 152 sid. ISBN 91-554-2938-6.

En enkel räkneövning visar att de flesta djur har förmågan att redan efter ett begränsat antal generationer av oförhindrad fortplantning och maximal överlevnad uppfylla jorden. Nu vadar vi ju inte runt i ett knädjupt myller av talgoxar eller taxar, eller irrar omkring i en skog av giraffer. Anledningen är helt enkelt den att alla djur som föds kommer antingen att dö innan de hinner skaffa egna ungar eller hindras att skaffa så många ungar som de teoretiskt sett skulle ha kunnat. Orsakerna härtill kan variera men generellt kan man skylla på ekologiska faktorer som att maten tar slut eller att ren platsbrist uppstår. Darwin insåg att detta kunde vara den drivande kraften bakom all biologisk evolution. Ifall det finns en systematisk skillnad mellan vinnare och förlorare i överlevnadsspelet kommer i det långa loppet det att leda till att egenskaper som gynnar överlevnad och fortplantning blir vanligare och att mindre gynnsamma drag försvinner från arten. Därigenom kommer arten att i ökande grad anpassas till sina ekologiska villkor. För att detta skall hända krävs att egenskaperna åtminstone till en viss procent är ärftliga och under genetisk kontroll. I ljuset av dagens kunskap visste Darwin nästan ingenting om genetik men mycket om ekologi och lyckades formulera en teori om biologisk evolution och artbildning som både i stort och smått har visat sig hållbar och fruktsam nu i 137 år.

På femtiotalet insåg man att genetiska processer är av fundamental betydelse för att förstå hur evolution kan uppstå genom den av Darwin föreslagna mekanismen, det naturliga urvalet. De flesta av den nya syntesens slutsatser och efterföljande insikter grundar sig på undersökningar i laboratorier. Ofta studerades bananflugor i laboratorier eller undersöktes andra mera sällan studerade arter under naturliga förhållanden, vilka hade en tidigare nästan helt okänd ekologi. Man kan inte studera evolution utan att ta hänsyn till både ekologiska och genetiska faktorer, vilkas samspel är evolutionens främsta drivkraft.

Det är sådana funderingar som dyker upp när man läser avhandlingen av Kjell Larsson, som har befunnit sig mitt i denna korsning mellan ekologi och genetik när han har studerat en population vitkindade gäss. Denna avhandling är en av två nyutkomna avhandlingar från Zoologiska institutionen i Uppsala, vilka behandlar de vitkindade gässen som i början av 70-talet etablerade sig på Gotland. Pär Forslund, vars avhandling redan presenterats i Ornis Svecica (nr 1, 1993), och Kjell Larsson har delat både på fältarbetets långa timmar i gömslet och uppsatsskrivandets födslovåndor.

Larsson och hans medarbetare fångade gässen under ruggningen i juli varje år från 1984 till 1991. Vid dessa tillfällen märktes alla fåglar, även årsungarna, samt åldersbestämdes och mättes de. Individmärkningen gjorde det möjligt att följa enskilda fåglars överlevnad och reproduktionsframgång, och framför allt att jämföra olika storleksmått, dels mellan fullvuxna ungar och deras föräldrar, dels mellan kullsyskon. Om man antar att föräldrar och ungar eller helsyskon liknar varandra av den enkla anledningen att de i genomsnitt har hälften av alla sina gener gemensamma så kan man tillämpa statistiska modeller från kvantitativ genetik för att räkna fram ärftligheten hos olika egenskaper. När man vet i vilken omfattning en egenskap är genetiskt styrd kan man med kunskap om karaktärens effekt på överlevnad och reproduktion förutspå evolutionens förlopp.

I Larssons avhandling rullas en detektivartad historia upp där han slutligen avslöjar förgripelsen på ett dolt antagande som boven i dramat med den frånvarande evolutionen mot större kroppsstorlek hos de vitkindade gässen. Larsson visar att större gäss får fler återvändande ungar än gäss med mindre kroppsstorlek. En anledning kan vara att större fåglar kan ha större fettreserver när de anländer till häckningslokalen. Det vill säga att naturligt urval gynnar större kroppstorlek. Dessutom är kroppsstorleken ärftligt betingad och därmed borde de vitkindade gässen bli större och större. På vägen fram till dramats upplösning avslöjar Larsson flera intressanta uppgifter om gässens ekologi och framför allt om genetiska faktorer. Ett av de mest anmärkningsvärda resultaten är att graden av ärftlighet varierar med födotillgången under uppväxttiden. Under dåliga år var ärftligheten för kroppsstorlek mycket lägre än under normala och goda år. Anledningen härtill är okänd men andra studier har gjort liknande observationer och en föreslagen orsak går ut på att ungarna kanaliserar mindre resurser till kroppstillväxt under dåliga år och därmed inte når upp till sin "förprogrammerade" kroppsstorlek.

I observationen att ärvbarheten kan påverkas direkt av miljön ligger också lösningen till gåtan om den uteblivna evolutionen mot ökad kroppstorlek. Det visar sig att en del av ärftligheten kan förklaras av att mödrarna har en tendens att ta sina ungar till samma födolokal dit de själva blev förda av sin mor när de var små. Detta leder till att ungarna kommer att likna sina mödrar, inte enbart på grund av att de har samma genetiska anlag, utan även på grund av att de har delat uppväxtmiljö. Dessutom påverkas kroppstorleken av om ungarna kläcktes tidigt eller sent på säsongen och det verkar som om det snarare är den senare faktorn som påverkar ungarnas framtida reproduktionsframgång än deras genetiskt "förprogrammerade" kroppstorlek.

Larssons arbete med de vitkindade gässen har en stor betydelse för vår förståelse av hur gener och miljö samtidigt formar individen. Läsningen är en nyttig påminnelse om att det som står skrivet i generna ibland kan vara lika osäkert som det som står skrivet i stjärnorna.

MATS GRAHN

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