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Impact of mustelid predation and ambient temperature on breeding success and population dynamics of Pied Flycatchers *Ficedula hypoleuca* in Swedish Lapland, 1965–2019

Påverkan av vesslor och temperatur på svartvita flugsnapparens Ficedula hypoleuca häckningsframgång och populationsdynamik i Lappland 1965–2019

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THE BREEDING SUCCESS of a nest-box breeding population of Pied Flycatcher *Ficedula hypoleuca* in subalpine birch forest in Swedish Lapland was studied over 55 years, with emphasis on the impact of small mustelids and ambient temperature during egg laying, incubation, and brood care. The proportion of nests predated was used as an index for mustelid abundance. Breeding failures were either total, due to breeding interruptions, or partial due to partial hatching failure or nestling death. Overall, mustelid abundance explained the rate of breeding interruptions at any breeding phase, but not when seasons with exceptional (>10%) predation rates were excluded. Variation in the rate of partial failure was unrelated to mustelid abundance. Climatic conditions affected clutch size, rate of breeding interruption, and partial loss of clutches or broods, with particularly pronounced effects during the incubation period. The mustelid abundance and weather conditions also influenced rates of nest-box occupation in subsequent breeding seasons, and the next-box population dynamics covaried with surrounding populations.

Keywords: climate | nest-box studies | long-term studies | subalpine birch forest | passerine

Citation: Nyholm NEI. 2024. Impact of mustelid predation and ambient temperature on breeding success and population dynamics of Pied Flycatchers *Ficedula hypoleuca* in Swedish Lapland, 1965–2019. *Ornis Svecica* 34: 175–191. https://doi.org/10.34080/os.v34.24303. Copyright: © 2024 the author(s). This is an open access article distributed under the CC BY 4.0 license, which allows unrestricted use and redistribution, provided that the original author(s) and source are credited. The Pied Flycatcher Ficedula hypoleuca has during the latest two centuries expanded its distribution range to become a frequent breeder in an increasing part of Scandinavia (cf. Lundberg & Alatalo 1992). The subalpine birch forests occurring in northern Fennoscandia represent the most peripheral habitats within its range (Keller et al. 2020). In this habitat, the Pied Flycatcher is a relatively new inhabitant and encounters environmental conditions to which it might not be well adapted. The populations are exposed to unpredictable and strongly varying, often harsh climatic conditions, which strongly influence the breeding course and success (Järvinen 1983, 1986, 1989, Järvinen & Väisänen 1984, Thingstad 1997, Nyholm 2011). Furthermore, in the subalpine habitat they experience strongly varying and cyclic nest-predation pressure from small mustelids, least weasel Mustela nivalis and stoat M. erminea, because of the typically marked microtine population cycles. Thus, nest predation and the climatic conditions are the most obvious local factors that affect the breeding course in this habitat. The breeding Pied Flycatcher populations usually have failed to produce enough fledglings to be self-reproducing (Nyholm 2011). This paper is aimed to show how the yearly variations of mustelid abundance and weather affected the breeding output during its different phases, egg laying, incubation, brood care, and fledging, and their implications on the population dynamics during fifty-five breeding seasons, in 1965–2019.

Material and methods

The study was performed in 1965–2019 in a nest-box breeding population of Pied Flycatcher in subalpine birch forest at about 500-650 m a.s.l on the southerly facing slopes of the mountains Vallienjuoná and Gájssietjåhkka ($65^{\circ}58'N$, $16^{\circ}E$), about 5–10 km west of Ammarnäs, Swedish Lapland. The habitat is a predominantly rich type of birch forest, with luxuriant undergrowth of herbs ('meadow type'). In dryer parts, the forest turns into a 'heath type'. The habitats of the study area, which were considered stable during the study period, are similar to that of the mountain slope as a whole (cf. Enemar *et al.* 2004).

The nest boxes (for numbers and dimensions, see Nyholm 2011) were inspected regularly and enough often each season to register the number of breeding

attempts, egg laying, clutch and brood sizes, hatching success, and the number of fledglings. 'Breeding attempt' is assigned to nests with at least one egg produced, i.e., it included nests which were abandoned during the egg-laying phase. The rate of rebreeding after nest abandonment (only 25 verified cases in total) is considered negligible.

Events detrimental to the breeding course, such as nest abandonment, nest predation, reduced hatching success and nestling survival were noticed at the nest inspections. Breeding success is presented as the yearly mean number of fledglings per breeding pair.

Nest predation, predominantly by least weasel and stoat, occurred at any breeding phase (egg laying, incubation, and nestling periods). Disappearance of all the eggs or remaining eggshells (often perforated by canine teeth), or total loss of nestlings well before normal timing of fledging, were judged to be reliable signs of nest predation. Contemporary predation of parent birds (usually females) was revealed from occurrence of excess feathers, bitten off wings or legs within or close to the nest box. The yearly rate of predated nests is used as a proxy for the abundance of mustelids in the breeding habitat. Thus, the variable mustelid abundance is given as an index from o to 100, corresponding to the yearly rate (%) of predated nests.

The study included a period with exceptionally high nest-predation rates (>10%, cf. Järvinen 1990), in total 25 years, roughly from the mid-1980s to 2010, which culminated in the mid-1990s (Figure 1).

The beginning of the period with very high predation rates coincided with a severe outbreak of an epizootic mange among foxes (competitors to mustelids) in the 1980s (cf. Nyholm 2011). Towards the end of the study period the nest-predation rate showed a decreasing trend, to levels like those at the beginning of the study. The period of strongly increased nest predation by small mustelids is thus regarded as episodic, though long-lasting, and the levels of nest-predation rate are considered as exceptional for the habitat. The analyses of the influence of the mustelid abundance index on the breeding performance therefore apply to (a) the total study period (n = 55 seasons), with the observed levels of nest predation; (b) the total study period after excluding the predated nests (n=55 seasons), to illustrate possible influence of the actual mustelid abundance on breeding performance besides nest predation;



FIGURE 1. Variation in the yearly rate of predated Pied Flycatcher Ficedula hypoleuca nests (index of mustelid abundance), 1965–2019. The dashed line is from a cubic regression model.

— Variation i årlig predationsgrad hos svartvita flugsnapparen Ficedula hypoleuca 1965–2019 (index över förekomsten av vesslor). Den streckade linjen illustrerar en kubisk regressionsmodell.

and (c) the seasons (n=30) with nest predation rates considered as 'normal' for the study area (0-10%).

A negligible number of breeding attempts were interrupted by Wrynecks *Jynx torquilla* (23 cases) or bank voles *Clethrionomys glareolus* (one case).

Eggs that did not hatch after full time incubation were defined as unfertilized if the yolk had remained its original size, distinctly separated from the albumen by the vitelline membrane (the albumen then still being clear). Embryo death was established where the egg contents instead got more or less disintegrated.

Yearly, a number of females produced egg(s) with defective shell (Nyholm 1981, 2011). Their nests were restricted to the shore zone of the lake Stor-Tjulträsk. These clutches deviated by being smaller and that they were more frequently abandoned. They are considered atypical for the subalpine birch forest as a whole and are therefore not further considered. Also, a few failed breeding attempts were excluded as they obviously were caused by the investigation itself.

Climatic data were obtained for 1965–2014 from the Swedish Meteorological and Hydrological Institute (SMHI, cf. Nyholm 2011). The daily mean temperature during the yearly defined periods of egg laying, incubation, and brood care, respectively (Figure 2a–c), are used in the analyses of the effect of temperature on breeding performance. The egg-laying period is defined as the dates from the start to the end of laying of the population. The period of incubation starts six days (approximative clutch size) after laying start and lasts till laying ends. The nestling periods is set to start fourteen days (approximative incubation length) after the initiation of incubation and end fourteen days after the end fourteen days (approximative length of brood care) after the end of the incubation period. The variation of the yearly timing of egg laying is illustrated in Figure 3.

Correlation and regression tests (linear and cubic) are applied. All significance tests (Pearson's and linear regression analysis) are two-tailed and corrected r² values are presented. The software SPSS v. 23 was used.

Results

Nest predators (small mustelids) and strong variation of the ambient temperature within and between the seasons evidently affected the breeding course of the Pied Flycatcher during the study period. These environmental factors contributed to greatly varied and often poor breeding result. From on average 5.47 eggs laid in 5,391 complete clutches in 1965–2019 only 2.95 young per nest fledged (53.9%; Figure 4).

CLUTCH SIZE

The yearly mean clutch sizes varied between 4.80 and 6.40 eggs (CV = 15%; Figure 4) and was strongly related



FIGURE 2. Yearly mean day temperatures 1965–2014, during (**a**) the egg-laying phase (linear regression: r^2 =0.000, b=-0.003, p=0.91), (**b**) the incubation phase (linear regression: r^2 =0.005, b=-0.031, p=0.051), and (**c**) the nestling phase (linear regression: r^2 =0.000, b=-0.002, p=0.92) of the Pied Flycatcher *Ficedula hypoleuca*.

- Årliga dagsmedeltemperaturer 1965-2014 under den svartvita flugsnapparens Ficedula hypoleuca (**a**) äggläggningsfas (linjär regression: $r^2 = 0,000$, b = -0,003, p = 0,91), (**b**) ruvningsfas (linjär regression: $r^2 = 0,059$, b = -0,031, p = 0,051), och (**c**) boungefas (linjär regression: $r^2 = 0,000$, b = -0,002, p = 0,92).

to the yearly mean dates of laying initiation, which in turn varied with the dates of female arrival and ultimately with temperature in the end of May-beginning of June (for data on this, see Nyholm 2011). The yearly mean dates of laying start in 1965–2019 varied from 30 May to 14 June.

INTERRUPTED BREEDING

Breeding was initiated in 6,111 nests in 1965–2019. Of these, breeding failed in 2,719 (44.5%) nests, of which 1,065 were predated and 1,654 were interrupted for unverified reasons, during the egg laying, incubation or nestling periods (Figure 5a). The yearly variation in the



FIGURE 3. Variation of the yearly mean date for start of Pied Flycatcher *Ficedula hypoleuca* egg laying, 1965–2019 (1=1 May; 30=30 May). - Variation i årligt medeldatum för äggläggningens start hos svartvit flugsnappare Ficedula hypoleuca 1965–2019 (1=1 maj, 30 = 30 maj).

rate of interrupted breeding was great (CV = 51%), and 61% of the variation could be explained by the variation in the mustelid abundance index (linear regression: $r^2 = 0.609$, b = 1.010, p < 0.001). During the thirty seasons with nest predation rate $\le 10\%$, 1,064 breeding attempts out of 3,479 were interrupted (30.6%). The great yearly variation in the rate of nest interruptions (CV = 55%) showed no trend over these seasons (Figure 5b), but the variation was positively and close to significantly

correlated with the index of mustelid abundance (linear regression: r² = 0.093, b = 1.690, p = 0.056).

INTERRUPTED BREEDING DURING THE LAYING PERIOD

Laying was interrupted in 855 out of 6,091 nests (14.0%). The yearly rate of interrupted laying varied greatly (CV = 73%; Figure 6). Multiple stepwise linear regression analysis showed that the rate of interrupted



FIGURE 4. Variation in the yearly mean clutch size (black) and number of fledglings (red) of Pied Flycatcher Ficedula hypoleuca in 1965–2019. — Variation i den genomsnittliga äggkullstorleken (svart) och antalet flygga ungar per kull (röd) av svartvit flugsnappare Ficedula hypoleuca 1965–2019.





— Variation i andelen avbrutna h\u00e4ckningar (\u00f6vergivna bon) hos den svartvita flugsnapparen Ficedula hypoleuca under (a) samtliga \u00e4r (kubisk regression) och (b) \u00e4r d\u00e4 andelen r\u00f6vata bon var 0-10% (linj\u00e4r regression).

breeding during the laying phase was significantly and positively related to the variation in the index of mustelid abundance ($r^2 = 0.550$, b = 0.429, p < 0.001, n = 50).

Also the yearly mean daily temperatures during the egglaying periods affected the rate of interrupted breeding, with a higher frequency of failed attempts during the



FIGURE 6. Variation in the yearly rate of interrupted breeding during the egg-laying phase of the Pied Flycatcher Ficedula hypoleuca in 1965–2019 (cubic regression).

Variation i årlig andel avbrutna h\u00e4ckningsf\u00f6rs\u00f6k under \u00e4ggl\u00e4ggningsfasen hos svartvita flugsnapparen Ficedula hypoleuca 1965–2019 (kubisk regression).

egg-laying phase in relatively cold springs (partial correlation: r = -0.437, p = 0.002, n = 50).

When excluding the predated nests, 517 out of 5,752 nests (9.0%) were abandoned in 1965–2019, with a large variation between years (CV = 67%). A multiple stepwise linear regression analysis showed that the index of mustelid abundance still contributed significantly to the yearly variation of nest abandonment, but the slope was much smaller ($r^2 = 0.171$, b = 0.165, p = 0.002, n = 50). Also, yearly mean daily temperature during laying periods affected the rate of abandonment (partial correlation r = -0.428, p = 0.002, n = 50). In the 30 seasons when the mustelid abundance was 'normal' for the habitat (index ≤ 10), 287 out of 3,479 (8.2%) breeding attempts were interrupted during the laying phase. For these 30 seasons, the variation in the yearly rate of interruption was not related to the variation of yearly mean daily temperature in 1965-2014 (p = 0.13, n = 26), nor to the mustelid abundance index (p = 0.20, n = 30).

INTERRUPTED BREEDING DURING THE INCUBATION PERIOD

In the years 1965–2019, 1,157 out of 5,256 breeding attempts (22%) were interrupted during the incubation period. Of these, 470 nests were predated and 687 abandoned for unconfirmed reasons. The yearly loss varied

greatly (CV=77%; Figure 7). Multiple stepwise linear regression analysis revealed that the variation in the mustelid abundance index accounted for 67% of the variation of breeding interruption (r^2 =0.67, b=0.879, t=9.719, p<0.001). The variation of the yearly daily mean temperature during incubation also contributed significantly to the variation, with a higher rate of abandonments in cold springs (partial correlation: r=-0.338, p=0.018, n=50). The rate of abandoned clutches varied greatly between years (CV=66%; Figure 8a).

Multiple stepwise linear regression analysis showed that the variation in mustelid abundance index and yearly mean temperature during the incubation periods in 1965–2014, both contributed significantly to the variation in the rates of clutch abandonment (mustelid abundance: $r^2 = 0.227$, b = 0.315, p = 0.001; temperature (partial correlation): r = -0.413, p = 0.003, n = 50). Together they explained 35% of the variation in the nest abandonments. In the 30 seasons with 'normal' levels of mustelid abundance index, 394 out of 3,193 breeding attempts were interrupted (12.3%; Figure 8b).

In the years with 'normal' predation only 43 breeding interruptions were due to nest predation, The yearly rate of interrupted breeding was significantly correlated with yearly daily mean temperature (r^2 =0.301, b=-2.905, p=0.002, n=25; Figure 9).



FIGURE 7. Variation in the yearly rate of interrupted breeding during the incubation phase of the Pied Flycatcher Ficedula hypoleuca in 1965–2019 (cubic regression).

Variation i årlig andel avbrutna häckningsförsök under ruvningsfasen hos svartvita flugsnapparen Ficedula hypoleuca 1965–2019 (kubisk regression).



FIGURE 8. Association between nest abandonment (excluding predation events) during the incubation in the Pied Flycatcher Ficedula hypoleuca and predation rate (%) in 1965–2019: (a) all years (linear regression), (b) years with "normal" mustelid abundance, with nest predation rate of 0–10%. – Förhållandet mellan andel övergivna bon (exklusive rövade bon) under ruvningsperioden hos svartvita flugsnapparen Ficedula hypoleuca och andel rövade bon (%) 1965–2019 (linjär regression) för (a) samtliga år och (b) år då med "normal" förekomst av vesslor i habitatet (med 0–10% rövade bon).

INTERRUPTED BREEDING DURING THE NESTLING PERIOD

In clutches where at least one young hatched, breeding interruption during the nestling period due to nest predation (and for unverified reasons) included 707 out of 4,099 nests (17%) in 1965–2019. The variation over the years was again great (CV = 86%; Figure 10).

Multiple stepwise linear regression analysis revealed that both the index of mustelid abundance and the yearly mean daily temperature during the nestling periods accounted for significant parts of the interruptions during the nestling periods (r^2 =0.099, b=0.330, p=0.015 and partial correlation: r=-0.307, p=0.032, n=50).

Out of 3,832 broods, 457 were abandoned (11.9%). The yearly rate of abandonment varied greatly (CV=111%), being significantly explained by the yearly mean temperature during the nestling phase (r^2 =0.068, b=-2.534, p=0.038, n=50; Figure 11) but statistically unrelated to the yearly variation in mustelid abundance index (p=0.94).

In the years with 'normal' mustelid abundance index, 383 broods out of 2,783 were interrupted (13.8%). The yearly variation of interruption (CV 101%) was insignificantly explained by the variation in yearly mean daily temperature (p=0.28, n=26) as well as the index of mustelid abundance (p=0.53, n=30).



FIGURE 9. Variation in the yearly rate of interrupted breeding of the Pied Flycatcher Ficedula hypoleuca in relation to the yearly mean temperature during the incubation phase, at nest predation rate 0–10%, in 1965–2014.

 Variation i årlig andel avbrutna h\u00e4ckningsf\u00f6rs\u00f6k hos svartvita flugsnapparen Ficedula hypoleuca i relation till den \u00e4rliga medeltemperaturen under ruvningsf\u00e4sen, vid bopredationsgrad 0-10% under 1965-2014.

PARTIAL HATCHING FAILURE AND LOSS OF NESTLINGS

Breeding success was also reduced by unhatched eggs. In 1965–2019, unhatched eggs were found in 1,586 out of the 3,885 clutches (40.3%) in which at least one egg hatched. The coefficient of variation between years was 27% (Figure 12).

In total, 2,489 eggs out of 21,234 did not hatch (11.7%). Multiple stepwise linear regression analysis revealed that the variation of the yearly rate of nests with unhatched eggs in 1965–2014 was significantly explained by the variation in yearly mean temperature during the incubation period ($r^2=0.172$, b=-3.032, p=0.002; Figure 13) but was unrelated to the variation in mustelid abundance index (partial correlation: p=0.53).

Hatching failures of individual eggs were due to eggs being unfertilized or to embryo death. The incidences of each of these reasons were studied in 614 of the clutches with partial hatching failure in the years 1969– 2019. Unfertilized eggs occurred in 275 (44%) and



FIGURE 10. Variation in the yearly rate of breeding interruption (including predation) in the Pied Flycatcher Ficedula hypoleuca during the nestling periods in 1965–2019 (cubic regression).

-Variation i årlig andel avbrutna häckningsförsök (inklusive prederade bon) hos svartvita flugsnapparen Ficedula hypoleuca under boungefasen 1965–2019.



FIGURE 11. Yearly rates of abandoned broods (excluding predated broods) of the Pied Flycatcher Ficedula hypoleuca in relation to yearly mean temperature during the nestling period, 1965–2014 (linear regression).

 Variation i årlig andel övergivna ungkullar (exklusive rövade kullar) hos svartvita flugsnapparen Ficedula hypoleuca i relation till den årliga medeltemperaturen under boungefasen 1965–2014 (linjär regression).

dead embryos in 379 of the clutches (61%). In total 339 eggs (range: 1–6 per clutch) were unfertilized and dead embryos occurred in 538 eggs (range: 1–6 per clutch). In 40 clutches I found both unfertilized eggs and eggs with dead embryos. In 15 of the clutches (2.4%) (containing 3 to 6 eggs), all eggs were unfertilized as revealed after full time incubation. In 596 broods out of 3,366 (16.9%)

in 1965–2019, did some of the nestlings in a brood die, in total 996 nestlings. The yearly variation in partial nestling loss was great (CV = 79%).

Multiple linear regression analysis revealed that the variations in yearly mean temperature as well as in index of mustelid abundance the during the nestling phase had insignificant influence on the variation in rate



FIGURE 12. Yearly variation in the rate of partially unhatched clutches of the Pied Flycatcher Ficedula hypoleuca in 1965–2019 (linear regression). – Variation i årlig andel av partiellt okläckta äggkullar hos svartvita flugsnapparen Ficedula hypoleuca under 1965–2019.



FIGURE 13. Relationship between the yearly rates of unhatched eggs in partially unhatched clutches of the Pied Flycatcher Ficedula hypoleuca and the mean temperature during the incubation period in 1965–2014 (linear regression).

 Relationen mellan den årliga andelen okläckta ägg i partiellt okläckta äggkullar hos svartvita flugsnapparen Ficedula hypoleuca och medeltemperaturen under ruvningsfasen 1965–2014 (linjär regression).

of nests with partial nestling death: b = -1.042, p = 0.36and b = -0.117, p = 0.25, respectively.

RELATION BETWEEN BREEDING SUCCESS AND POPULATION DEVELOPMENT

The variation in the yearly the nest-box occupation rates in year X+1 (1966–2019) was significantly correlated with the mean number of fledged young in year X (1965–2018, linear regression: $r^2=0.122$, b=4.142, p=0.006, n=54; Figure 14). The corresponding positive correlation also held for yearly nest-box occupation rate in year X+2 ($r^2=0.104$, b=3.790, p=0.011).

Also, the index of mustelid abundance and yearly mean temperature during incubation in year X, were significantly related to the variation in occupation rate both in year X+1 ($r^2 = 0.285$, b = -0.415, p < 0.001 and partial correlation: r = 0.410, p = 0.003, n = 50) and year X+2 ($r^2 = 0.192$, b = 0.338, p < 0.001and partial correlation: r = 0.301, p = 0.036) according to multiple linear regression analysis. Together these two factors accounted for 39% and 25% of the variation in occupation rate in year X+1 and year X+2, respectively. In contrast, the yearly mean temperatures during the laying and nestling periods in year X were not significantly correlated to the variation in occupation rate in either year X+1 (p = 0.62 and p = 0.56, respectively) or year X+2 (p = 0.10 and p = 0.09, respectively).

Then looking at seasons with only 'normal' mustelid abundance index linear regression analysis revealed that the variation of the yearly average temperatures during incubation and nestling periods in year X significantly influenced the occupation rate of the nest boxes in year X+1 ($r^2 = 0.192$, b = 3.438, p = 0.015 and $r^2 = 0.209$, b = 3.658, p = 0.011, n = 26) while the index of mustelid abundance did not (p = 0.65).

Discussion

Pied Flycatcher populations breeding in the subalpine birch forest, thus breeding at the northern and altitudinal limits of their range, are known to experience great problems to produce enough offspring to be selfreproducing (Järvinen 1989, Nyholm 2011). Climatic conditions during the breeding season, typically being strongly variable and often harsh, are recognized to account for a significant part of the reduced breeding success of the species (Järvinen & Väisänen 1984). The actual habitat in northern Sweden is also characterized by the occurrence of greatly varying and cyclic small rodent populations which typically crash every third or fourth year. The then built-up mustelid populations



FIGURE 14. Relationship between the yearly number of fledglings per breeding pair of the Pied Flycatcher *Ficedula hypoleuca* (in year X) and nestbox occupation rate the following year (year X+1) during 1965–2019 (linear regression).

— Relationen mellan det årliga antalet flygga ungar per h\u00e4ckning hos svartvita flugsnappare Ficedula hypoleuca (\u00e4r X) och holkbes\u00e4ttningsgrad under det n\u00e4stf\u00f6ljande \u00e4ret (\u00e4r X+1) 1965–2019 (linj\u00e4r regression).

need to exploit alternative food items, which among others also include nest-box breeding Pied Flycatchers, their eggs and young (Järvinen 1990, Nyholm 2011).

The aim of this study was to estimate the effect of these local environmental factors, i.e., harsh weather and mustelid abundance, on breeding success of pied flycatchers during different stages and, as an extension, the population development.

CLUTCH SIZE

The clutch size of the Pied Flycatcher, which is ultimately limiting the breeding outcome, is strongly related to the time schedule of the egg laying so that later laying initiation means smaller clutches (cf. Nyholm 2011). The northern position and the relatively high altitude of the study area incurs an increased risk of hazardous spring weather. Egg formation, in the subalpine habitats at Ammarnäs and in northern Finland, is triggered only after the daily mean temperature reaches about 6°C (Järvinen 1983, Nyholm 2011). Lower temperatures frequently lead to delayed start of egg laying and thus smaller clutches (cf. Järvinen 1989, Nyholm 2011). This will reduce the number of fledglings, thereby closing in on the numbers needed for self-maintenance of the population (4.4 fledglings per breeding pair, as estimated by Järvinen 1983).

The mean size of complete clutches in Ammarnäs in 1965–2019 (n = 5,256) was 5.47 eggs from which on average 2.95 fledglings were produced. Including the 855 nests in which breeding were interrupted during egg laying, the mean number was 2.54 fledglings per breeding pair. The number needed for self-maintenance of the population was reached in only 3 of the 55 seasons (Figure 3). The insufficient production of young was mainly a consequence of total loss of eggs or broods. In addition, 40% of the remaining egg clutches were struck by partial losses due to death of embryos or failed fertilization and 17% of the broods were struck by partial nestling death.

INFLUENCES OF THE MUSTELID ABUNDANCE ON BREEDING SUCCESS

Nest predation, the plundering of all eggs or nestlings, was the dominant restricting factor of breeding success in 1965–2019. On average, $15.7\% \pm 17.5$ (SD) of the breeding Pied Flycatcher pairs suffered from nest predation during the egg laying, incubation and brood care periods. The variation in nest predation during the periodically exceptionally high mustelid abundances accounted for 46% of the variation of the yearly numbers of fledglings. The mean rates of breeding interruptions were 14% during the laying period, 22% during

incubation, and 17% during the nestling period. Nest predation as the reason for failed breeding attempts occurred most frequently during the egg laying and incubation phases. It then accounted for 45% and 67%, respectively, of the yearly variation in breeding failure. It also accounted for a significant part, 12%, during the nestling period. When excluding the predated nests from the calculations, the mean rates of interruption was 9% during the laying period, and 14% and 12% during the incubation and nestling periods, respectively. The yearly variation in mustelid abundance index then still explained significant parts of the variation in nest abandonment during the laying and incubation periods, 17% and 23%, respectively.

During the nestling period, however, the variation of the rate of abandonments was unrelated to the yearly variation in the index of mustelid abundance. It is tempting to suggest that the Pied Flycatcher females were more easily disturbed enough to leave their nests by the mere existence of high mustelid abundance in the breeding habitat during the early breeding phases. It may also be that increased numbers of mustelids in the habitat led to more females being predated outside their nests. During the thirty breeding seasons with 'normal' mustelid abundance, the rates of abandoned nests were 8% during the laying period, and 12%, and 14% during the incubation and nestling periods, respectively. Then, the yearly variation of the rates of nest abandonment were insignificantly related to the variation of mustelid abundance at all of the breeding phases. This should mean that the mustelid abundance at 'normal' levels would have little influence on the rate of nests, totally or partially, spoiled due to mustelids. Thus, mustelids at 'normal' population levels would have only a marginal influence upon the overall breeding success.

INFLUENCE OF AMBIENT TEMPERATURES ON BREEDING SUCCESS

The strongly varying and frequently harsh weather conditions, with low temperatures, especially when combined with continuously rainy periods (cf. Nyholm 2011), did significantly impair the breeding success of the Pied Flycatcher. That was probably mainly due to interference with reduced availability of suitable food items for this insectivorous species. Climatic factors significantly affected all the breeding stages, i.e. egg formation, clutch size, incubation, hatching, and brood care. At periods with detrimental weather, females could temporarily pause egg laying, incubation, or brood care, with hatching failures and nestling deaths as results; cf. Pulliainen *et al.* (1994). At prolonged periods of harsh weather, parents could even abandon their nests for good. Very few females were shown, or could be suspected, to rebreed after nest abandonment after having started laying. During the laying period, the yearly variation of the rate of abandoned nests was negatively but insignificantly correlated to the variation of mean temperature. The mustelid abundance then posed the dominating threat to completed egg laying.

During the incubation period, the variation in the yearly mean temperature and the mustelid abundance did separately account for significant parts of the variations of the rate of breeding interruption. Together they then explained as much as 70% of the breeding failures. However, during the seasons with 'normal' mustelid abundance, only the yearly mean temperature variation explained a significant part (26%) of the variation in abandonment rate. During the nestling period, however, did neither temperature nor the index of mustelid abundance significantly influence the rates of breeding interruption the seasons with 'normal' mustelid abundance.

RELATION BETWEEN BREEDING RESULT AND THE POPULATION DYNAMICS

The variation in the nest-box occupation rates in year X+1 and year X+2, respectively, were significantly related to the yearly mean number of fledglings in year X. The rationale behind testing the influence over two seasons is that more than 90% of the breeding females annually recruited originated from outside the nest-box plots (Nyholm 2011), probably at the age of 2CY or 3CY, and that a significant proportion of Pied Flycatchers does not breed before the age of 3CY (Curio 1959, Harvey et al. 1985, Nyholm 1986). The yearly variations of the levels of the mustelid abundance and the ambient temperature during the breeding season, especially yearly mean temperature during the incubation period, did greatly influence the yearly breeding results in year X, and thereby also the yearly occupation rates of the nest-box breeding Pied Flycatchers in the next two seasons. The greater influence on the population dynamics of the variation of temperature during the incubation period than during the laying and nestling periods was tentatively due to more abandoned nests during incubation and the number of partial hatching failures due to embryo deaths. The latter loss struck at a rough estimate 1,500 eggs and was explained to a significant by mean temperatures during incubation.

During the years with 'normal' mustelid abundance, the yearly temperature during the incubation period in year X significantly influenced the size of the nestbox breeding population the subsequent season while mustelid abundance did not. That indicates that in these years the yearly temperature during the incubation phase normally is the only of the studied variables that influenced the dynamics of the nest-box breeding Pied Flycatcher population.

A comparison between the dynamics of the nestbox breeding population and the populations of the Pied Flycatcher outside the nest-box plots was possible thanks to contemporary territory mapping in the surrounding forest since 1963 (data from Enemar et al. 2004 for 1965-1999, and unpublished data from Göran Paulson for 2000-2019). The yearly variation of the population density of Pied Flycatcher territories, which closely equals the density of breeding pairs (Enemar et al. 1976), covaried significantly with the yearly variation of the nest-box occupation rate in 1965–2019 (Pearson correlation: r=0.599, p<0.001, n = 55). Multiple linear regression analysis revealed that the yearly mean temperature during incubation in year X accounted for a significant part of the territory density variation also in the forests surrounding the nestbox plots in year X+1 ($r^2 = 0.08$, b = 0.852, p = 0.026). In contrast to the yearly variation of nest-box occupation rate, territory density in the surroundings was insignificantly influenced by mustelid abundance in year X, (r = -0.184, p = 0.205). This suggests that the relatively sparse Pied Flycatcher population using natural holes for breeding was less exposed to nest predation by mustelids than was the about 40 times denser nest-box breeding population. During the years with 'normal' mustelid abundance, yearly mean temperature during incubation in year X was insignificantly related to the yearly variation of the territory density in year X+1 (p=0.44, n=26).

Yearly, about 90% of the nest-box breeding Pied Flycatcher females were recruited from outside the study area, probably at the age of 2CY or 3CY (Nyholm 2019). To have a significant impact on the nest-box occupation rate, and territory density in the birch forest surrounding the nest-box plots, the affecting factors could not only be strictly local but must have a concurrent impact in the larger population recruitment area. As judged from nestlings which were ringed in the nest-box plots or elsewhere and recovered as breeders, all showed faithfulness to subalpine habitats (Nyholm 2011).

The breeding course of the Pied Flycatchers breeding outside the nest-box plots was not studied. However, the parallel yearly population variation and that of the nest-box breeding population, together with the common relation to the ambient temperature, indicate similar variation of the yearly breeding results.

It is striking that the territory density of the Bluethroat Luscinia svecica (Enemar et al. 2004 for 1965-1999 and unpublished data 2000–2019) covaried with the territory density of the Pied Flycatcher at the study site (r = 0.536, p < 0.001), and with the frequency of the nest boxes occupied by Pied Flycatchers (r = 0.368, p = 0.006, n = 55). Moreover, the variation of the yearly mean temperature during the incubation phase (probably roughly similar to that of the Pied Flycatcher) in year X, accounted for a close to significant part of the variation in population density of the Bluethroat in year X+1 ($r^2 = 0.044$, b = 0.853, p = 0.077, n = 50), as revealed by multiple stepwise regression analysis. The yearly variation in the Bluethroat population density in year X was unrelated to the mustelid abundance in year X and year X+1 (p=0.51 and p=0.13). The (redspotted) Bluethroat, insectivorous like the Pied Flycatcher, breeds exclusively in Scandinavian subalpine habitats and could thus be expected to be well adapted to the climate conditions. For the Pied Flycatchers, in contrast, the subalpine habitats are at the northern and altitudinal margin of its breeding range and could therefore be expected to cope with the climatic challenges less well. But the significant covariation of their breeding populations and the significant relation to the ambient temperature, indicate that the breeding of the two species, unexpectedly, were similarly affected by the variable climatic conditions.

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Svensk sammanfattning

Häckningsförloppet hos en holkhäckande population av svartvit flugsnappare Ficedula hypoleuca studerades i subalpin fjällbjörkskog, med speciell inriktning mot påverkan av förekomst av småvesslor Mustela nivalis och hermeliner M. erminea (familj Mustelidae, underfamilj Mustelinae; framgent kollektivt refererade till som vesslor) och omgivningstemperatur under äggläggnings-, ruvnings- respektive boungeperioderna. I början och slutet av undersökningen hade förekomsten av vesslor en omfattning som anses vara 'normal' för biotopen, medan den i dess mellersta del såväl förekomsten som andelen rövade bon betraktas som onormalt hög. Temperaturförhållandena varierade kraftigt under och mellan häckningssäsongerna och var ofta ogynnsamma. Försämrade häckningsresultat berodde på att häckningar avbröts eller att de drabbades av att en del av äggen inte kläcktes eller att boungar dog.

METODER

Studien gjordes 1965–2019 i huvudsakligen rik fjällbjörkskog, ca 500–650 m ö.h. på sydsluttningarna av fjällen Vallienjuoná och Gàjssietjåhkka, 5–10 km väster om Ammarnäs. Varje år registrerades antal häckningar (bon med minst ett ägg), datum för äggläggningen, antal värpta ägg och kläckta och utflugna ungar. Ägg som inte kläcktes trots fullgången ruvning betraktades som obefruktade om ingen fosterutveckling skedde. Fosterdöd gällde om innehållet i de okläckta äggen blev mer eller mindre nerbrutet under ruvningen.

Antal avbrutna häckningar på grund av bopredation respektive okänd anledning noterades. Den årliga andelen rövade bon anses spegla mängden av vesslor i häckningsmiljön. Denna anges därför som index från o till 100. Förekomsten av vesslor varierade mycket mellan åren alltefter storleken hos den typiskt cykliskt varierande tätheten hos smågnagarpopulationerna i norra Skandinavien. Studien omfattade en period, i grova drag från mitten av 1980-talet till 2010 med onormal andel rövade bon (figur 1). Normal andel rövade bon i området anses vara högst 10%, vilket förekom under trettio av åren. Uppgifter om temperaturer erhölls från SMHI:s mätstationer i Ammarnäs eller andra jämförbara stationer i regionen för åren 1965–2014. Dygnsmedeltemperaturer under respektive häckningsperiod och år används vid beräkningarna (figur 2).

Förluster av ägg och ungar

Bopredationen och stora temperaturvariationer under och mellan häckningssäsongerna medverkade till att häckningsresultaten varierade kraftigt och oftast svar svaga. Från 5 391 kompletta äggkullar med i genomsnitt 5,47 ägg lämnade endast 2,95 ungar bona under 1965–2019 (figur 4). För att populationen skall anses vara självreproducerande krävs att i genomsnitt 4,4 ungar produceras. Det antalet uppnåddes endast under 3 av de 55 åren. De årliga kullstorlekarna varierade med temperaturen vid äggläggningens början.

Äggläggning påbörjades i 6111 bon 1965–2019, varav 2719 övergavs. Bopredation drabbade 1065 av bona medan 1654 övergavs av okänd anledning. Andelen avbrutna häckningar varierade kraftigt mellan åren (figur 5), till största delen beroende på variationen i förekomsten av vesslor. Under äggläggningsperioderna 1965–2019 lämnades 855 av bona. Både förekomsten av vesslor och årlig medeltemperatur bidrog signifikant till variationen av andelen avbrutna häckningar. Om man bortser från de bon som rövades av vesslor lämnades 517 av 5752 bon. Även då var variationen mellan åren i andelen lämnade bon signifikant förklarad av variationerna i förekomst av vesslor, och också medeltemperatur. Under ruvningsperioderna lämnades 1157 bon av 5256, med stor variation mellan åren (figur 7).

På grund av predation lämnades 470 bon medan 687 övergavs av okänd anledning. Den årliga andelen lämnade bon var i signifikant grad förknippad med variationen i förekomsten av vesslor såväl som de årliga medeltemperaturerna under ruvningsperioden. Detta gällde även då man bortser från de bon som rövades av vesslor. Under de 30 år då förekomsten av vesslor var på normal nivå (<mark>figur 8b</mark>) drabbade bopredation totalt endast 43 bon under ruvningsperioden.

Variationen i den årliga medeltemperaturen hade betydande samband med variationen i andelen lämnade bon (figur 9). Under boungeperioden övergavs 707 av 4099 bon under 1965–2019, med stor variation mellan åren (figur 10). Variationen förklarades signifikant av variationerna i både förekomsten av vesslor och medeltemperatur. Bortsett från rövade bon övergavs 457 av 3832 bon 1965–2019. Variationen i årliga medeltemperaturer under boungeperioden påverkade signifikant variationen i andelen övergivna bon (figur 11).

Till skillnad från förhållandena under äggläggnings- och ruvningsperioderna kunde inte påvisas att de häckande svartvita flugsnapparna under boungeperioden stördes av enbart förekomst en av vesslor i häckningsterrängen i den grad att de övergav sina bon.

Förluster av ägg och ungar förekom också i bon där en andel av äggen inte kläcktes trots full ruvningstid eller att boungar dog. Partiella förluster under ruvningsperioden drabbade 1586 av 3885 bon där minst ett ägg kläcktes. Totalt drabbades 2489 av 21234 värpta ägg i 1586 av 3885 bon (figur 12). Utebliven kläckning berodde antingen på att äggen var obefruktade eller drabbades av fosterdöd. I 614 undersökta kullar där en andel av äggen inte kläcktes befanns 1–6 ägg vara obefruktade i 275 kullar (totalt 339 ägg) och 379 kullar med döda foster i 1–6 ägg (totalt 538 ägg).

Andel kullar med partiell äggförlust varierade signifikant med de årliga variationerna i medeltemperatur under ruvningsperioden (figur 13), medan de partiella förlusterna av ungar inte hade samband med temperaturvariationerna under boungeperioden.

Påverkan på populationsdynamik

Utvecklingen hos holkpopulationen av svartvit flugsnappare samvarierade med hur många ungar som den producerade. Variationen i antal ungar som lämnade bona år X under 1965–2018 hade signifikant samband med populationsstorleken (andel holkar som var besatta) de två nästkommande åren (figur 14). Grunden till att testa sambandet under två år framåt är att en stor andel av svartvita flugsnapparhonorna börjar häcka först vid två års ålder (3K). De årliga variationerna av förekomst av vesslor såväl som temperaturen under ruvningsperioden (men inte under äggläggnings- eller boungeperioderna) under år X förklarade signifikant beläggningen i holkarna år X+1 och år X+2.

Slutsatsen blir att svartvita flugsnapparens häckningsresultat på fjällsluttningarna vid Ammarnäs 1965–2019, i periferin av artens utbredningsområde, begränsades betydligt av tidvis onormalt hög förekomst av vesslor och av de ofta förekommande låga temperaturer som rådde under äggläggnings-, ruvnings- och boungeperioderna. Påverkan av de studerade lokala omvärldsfaktorerna på häckningsresultaten hade även betydelse för svartvita flugsnapparens populationsdynamik.



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