

Biology of Alpine accentor (*Prunella collaris*) X. Chronological records of daily activities while breeding

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Abstract. Chronological notes on the daily life of *Prunella collaris* appear only fragmentary in the literature. During many years of work with this species in the Western Carpathians, some important fragments of the daily chronology of the species have been selected for this paper, which give zoologists, ethologists, parasitologists or even climatologists more detailed insight into how this bird species is adapted to conditions of the high mountains. For example, we have evidence that the transmission of mites, lice or fleas from males to females can take place during nest building, with not only the alpha but also the beta males inspecting the nest for several seconds, even though they are not building the nest. Even during this time, males and females can spend several seconds in the nest cavity. This work also adds to our knowledge of when nesting males are most aggressive and when they increase their feeding intensity on the nestlings in the nest. This occurs before the nestlings emerge from the nest. The work will also provide information on the effect of daily precipitation on nesting and the limiting factor of snowfall. The movement of chicks in the nest has been recorded and the notes contribute to knowledge of how the daily life of this species really pulsates during the breeding season.

Key words: Alpine accentor, *Prunella collaris*, nesting and breeding behaviour, West Carpathians

Spring occupation of nesting sites, transition from arrival to family ties

Northern slopes of Chopok and Dereše, May 3rd, 1986

11:30 One female on the eastern side of Chopok, the second on Kónský Grúň, the third below Dereše and males around them, splitting from the arrival aggregation into individual families is occurring, though birds still largely gathering food together during the day they are not yet building a nest, though males are singing intensively.

Territorial defence of the nest surroundings during nest construction

Kónský Grúň, July 5th, 1985

13:02 Alpha male feeding and guarding the nest area.
13:09 Alpha entered the nest and was there for about 20 seconds.
13:13 Alpha flew away, chasing the other male.
13:18 Appeared.
13:20 Appeared.
13:21 Female put nest material in cavity, was in cavity for about 20 seconds.
13:22 Alpha male and female mated twice outside the nest.
13:25 Alpha male flew away.
13:32 Alpha male flew in and was in the nest for about 20 seconds.
13:35 Alpha is guarding.
13:38 Male re-entered the nest and is modifying the nest (There may be the appearance here that the dominant male is also building the nest, however, his participation in nest building is minimal. However, frequent visits to the nest may already ensure the transmission of some ectoparasites).
13:39 Alpha has come out and is feeding.
13:42 Alpha heard another male singing and flew down to him to chase him away.
13:45 Four adults of the family arrived; three males and one female.
13:46 Alpha chased off another male.
13:48 Alpha chased off another male.
13:50 Alpha chased off another male.
13:52 Female arrived without nest material, entered nest cavity.
13:53 Alpha male chased off another male.
13:55 Alpha went into the nest cavity to join the female and then they both exited the nest.
13:56 Female started to collect and put nesting material in the nest.
13:58 Female entered the nest.
13:59 Alpha male frightened off the other male.
14:02 Alpha flew in, courting but not mating.
14:05 Alpha and female sitting over nest.
14:07 Alpha standing, guarding, female feeding.
14:08 Alpha chased off another intruder.
14:08 Alpha chased off another intruder.
14:09 Female collects nesting material, enters nest and flies out in 10 seconds.
14:10 Alpha chased off another male.
14:11 Alpha chased off another male.

Building the nest*Konský Grůň, July 6th, 1985*

10:00 - 10:03 Female and alpha drive away two more accentors.
 10:09 Both alpha and female are together in the nest.
 10:10 Female collects material and puts it in the nest.
 10:12 Female brings material to the nest, male joins her in the nest, and they remain inside for 17 seconds (possibilities for parasite transmission).
 10:13 Female brought nest material into nest.
 10:14 Beta male flew to the nest; female is outside looking curiously into the nest opening.
 10:15 Beta has flown away, and both female and alpha are feeding just below the nest while the third and fourth males are above the nest.
 10:17 All birds are feeding below the nest, there is reduced aggression between males when feeding.
 10:19 Alpha is feeding.
 10:25 Alpha and female are around the nest.
 10:26 Female returns with nesting material, 45 seconds depositing it in the nest.
 10:28 Beta individual spotted nearby.
 10:30 Female and alpha observed together near the nest.
 10:33 Female and alpha foraging near the nest and beta male entered the nest (this is how parasite transmission through the nest is possible from both the female and alpha male to weaker males).
 10:35 Alpha male chased away the beta male and then collected food with the female.
 10:37 Beta male re-entered the nest.
 10:38 Alpha male chased him away.
 10:41 Female flew in with nest material and both she and alpha went in, 20 seconds of putting material in the nest.
 10:41 They came out and gathered around the nest.
 10:45 Other males fly around the nest area.
 10:47 Main pair still at the nest, alpha singing.
 10:48 Alpha chased away a second male.
 10:48 Alpha chased away a second male.
 10:49 Female feeding.
 10:52 - 10:55 Four adult accentors feeding together.
 10:55 - 10:58 Five adult accentors feeding together, three males and two females.
 10:58 - 11:00 All five accentors feeding, followed by three males making high display flights.

The experiment with cooling the nestlings, chicks aged 2, 3, 3, 4 days*Dereše, July 15th, 1985*

13:40 Female returned with food and is sitting on the cubs.
 13:43 Male fed the chicks, he was in the nest for about 2 minutes, female was still sitting because the chicks were cold (through throat rings food had been taken out of the crops earlier), female sat until 14.00.
 14:00 Male came to feed the chicks, flew out of the nest, sang, fed the oldest chick with a small butterfly caterpillar.
 11.11 Female returned with food, exhibiting different behavior than the male. She walks around for about a minute, then enters the nest but immediately jumps out without feeding, then enters nest

but sticks her head out of nest cavity three more times. Following this she feeds and sits on young.
 14:11 Female was sitting, male came to feed, flew in singing, went straight into the nest (male was less careful to reveal the nest to predators than female) and flew away, immediately, singing, then came into the nest singing.
 14:25 The female was sitting (I came to the nest, took food from the crops of chicks and put the throat rings down) the female flew out as I approached the nest.
 14:45 The female came in; she only flew in twice and looked out of the nest, fed, and stayed perched on the chicks.

"Noon" feeding break for nestlings in nest, chicks at 3, 4, 4, 5 days old*Dereše, July 16th, 1985*

Weather: still foggy, visibility about 30 metres.
 11:37 A male flew in singing.
 11:45 - 11:53 A female walked alertly around the nest, chirping softly. Then she jumped into the nest to feed the young and stayed there.
 12:00 Male flew in and fed.
 12:05 Female flew out of nest.
 12:18 Female returned, fed and flew away.
 12:18 - 13:00 Male did not arrive, sang in wider area, with a range up to 200 m.
 13:10 Female flew in to feed in the afternoon, male singing below her.

Vigilance of the female to perceived danger, chicks 7,8,8,9 days old*Dereše, July 20th, 1985*

10:19 The female has come to feed but waits and does not feed. The older the chicks are, the more vigilant she is.
 10:25 The chicks are already soiling outside the nest on its edge.
 12:00 The female has fed.
 12:09 The male is singing below her.
 12:27 - 12:47 Female walks silently to the nest, moves around the nest in a radius of 1 - 2 m, noticeably quiet, deep call, lasting up to 20 minutes.
 12:47 Still feeding and taking out droppings simultaneously.

Snowfall. One chick, 5 days, snow as a limiting element of breeding extinction*Konský Grůň, June 2nd and 3rd, 1986*

June 2nd. 10 cm of snow overnight, in snow drifts up to 20 cm, the female incubated the chick and did not leave. During this time only the male feeds, but he must go to lower elevations for food, because the snow is at 1200 - 1300 metres and higher.
 The female took every moment to clean her feathers, but when she felt cold, because she was always close to the nest and it was in a hollow between the snow, she returned.
 She basked both the nest and the chick from inside, she was able to sit on the nest for prolonged peri-

ods, the chick was viable, it had no homeothermic metabolism yet.

June 3rd. Nest abandoned, male only lasted a day or so to feed, but nest must have been wet from snow, chick found dead.

Chick, 7 days old, care and feeding during weather changes in one day, nest under summit, two eggs unfertilised

Chopok, July 9th, 1988

12:00 A female came out from the bottom of the Chopok cauldron, the male wanted to mate with her.

12:23 Female came out again from below, fed briefly and immediately flew away with the male.

12:24 Next female feeding.

12:30 Male fed the young, then flew to the top of Chopok and sang.

12:44 Female fed, arrived with a long larva (Tipulidae), although she flew in from the right of the ridge, she always flies down below the nest, then comes sideways from the rock, goes in, feeds and immediately flies out after feeding.

13:00 The sun came up.

13:11 Female flew to the left about 5 metres below the nest, went into the nest, fed for about 10 seconds and brought out droppings, dropped them in flight about 5 metres from the nest.

13:45 Flew from above the nest from under the gable and then came from below to feed, fed briefly, flew out and immediately started collecting food, I saw her collecting for about 2 to 3 minutes.

13:45 - 13:48 The sun sets, quite cold.

13:50 She came with a faint call, fed briefly and flew down.

13:56 She came down from below the nest, entered the nest from below, fed for 20 seconds and then flew down.

14:05 Clouds and rain coming.

14:05 Female flew in from above from below, approached the nest for about 20 seconds, stayed in the nest for about 45 seconds, when male came in singing, he didn't feed, just looked in the nest and when he saw the female flew straight down, after 45 seconds the female also flew out, gathered under the nest for about two minutes, then met the male under the nest and flew away.

14:05 - 14:40 rain, clouds, fog.

14:40 Weather changes, sunny and nice.

14:50 Arrival from above, sunny, 10 seconds around nest, 5 seconds feeding, two males flew in behind her, all three flew away with a call.

15:05 Arrived, 5, 7 seconds around nest, 12 seconds feeding, brought up droppings in flight and released, chick whistled when fed.

15:10 Fed again and brought up droppings.

15:25 Reappeared from above, walked cautiously to nest for 30 seconds, then fed, flew out, brought up droppings. Weather fine, just frigid wind.

15:32 Came down from above below nest, went to nest for 21 seconds, fed for 15 seconds and flew out.

15:38 Came to feed for about 30 seconds, went to the nest, saw me, started warning calls, went into the nest, fed for 10 seconds, brought up droppings and every time she flies out of the nest she flies to the left. This means that the accentors often have

a standard flight path when they are feeding and flying out of the nest.

16:11 Again from above under the nest, went to the nest 28 seconds, fed 17 seconds, flew out with droppings to the left.

16:20 Arrived from left under nest, walked to nest for 35 seconds, heard young for about 20 seconds, i.e., being fed, then stayed in nest for 6 minutes, sat on them and warmed them up, flew off to left.

16:32 Male arrived, stayed for about 55 seconds, hesitated, then fed, then flew down with another male.

16:53 Female arrived from left and from below, walked to nest for 35 seconds, fed for 10 seconds and flew off to left.

16:59 Male flew in, waited 55 seconds, saw me, then fed for 3, 4 seconds and sang below.

17:00 Clouds and fog move in, female arriving from left, 15 seconds arrival to nest, 13 seconds feeding young, flew out, brought out droppings.

17:18 Both female and male arrive from below, female shaking and active to mate, calling. Male singing but not mating, male then flew down, female walking for 20 seconds, then stayed in nest for 2 minutes and 33 seconds, of which she fed for about 20 seconds, flew to the left and then a waiting male came from the right, flew into the nest immediately (the male flew into the nest more than he walked), fed for about 7 seconds and flew to the right.

17:20 Still in the clouds and the wind was moving out of the cauldron onto the ridge.

17:29 Male from above immediately flew down to nest, waits at nest for 3 seconds, feeds chicks for 12 seconds and flies off to the right.

17:45 Female came up from below, walking for about 5, 7 seconds and feeding for 20 seconds and stayed in the nest.

17:48 Male flew in from above, called to female, she flew out to left, male walked in for about 7 seconds fed and flew out to the right.

18:02 From left walking 10 seconds male came in, fed for 10 seconds, flew out, met another male, flew left to rock and singing.

18:03 Female walked 3 seconds straight to nest to feed, sat on chicks for 6 minutes and 10 seconds and flew off to left, by 18:21 they had not arrived, clearing skies.

A chick 8 days old, nest care on a rainy day

Chopok, July 10th, 1988

09:10 Female fed once, then sat in nest for 6 minutes. Outside was cold, cloudy, and rainy with strong wind from the valley.

09:16 Female left the nest, walking discreetly.

09:30 Male flew in, walked 2, 3 seconds, entered nest, fed for 8 seconds, flew away.

09:43 Female wanted to go straight to nest but saw my hand moving, went back under rock, waited another 5 seconds before going to feed, fed for 23 seconds, brought up droppings.

09:55 Male flew in (heavy fog), went to nest for 3 seconds, fed for 15 seconds, flew left.

10:10 Male flew in from above, waited 20 seconds, fed for 8 seconds and flew away.

10:20 Female came in from left, walked 10 seconds, fed and then sat for 5 minutes, would have sat lon-

ger but was frightened by falling rocks around nest, flew away left.

10:37 Male came to feed, waited 3, 4 seconds, male flew a shorter distance in front of medistance, fed for 8 seconds and flew down to nest.

10:42 Female came from below, up to the nest for up to 40 seconds, fed for 10 seconds fed for 10 seconds, flew down to valley.

10:55 Female came in from below, walked for 30 seconds and fed for 15 seconds. When she fed the chick she whistled. Then the male came in, walked for 3 seconds, fed for 5 seconds and flew down and in another 5 seconds the female also flew out and flew down into the cauldron, (i.e., both male and female were together in the nest for a few seconds, when the nest is in the clouds, the parents are hunting insects below the clouds).

11:12 Weather improving, sky clearing, female went to nest for below for 3, 4 seconds, fed for 23 seconds, flew left.

11:29 Female returned to nest for 3, 4 seconds, fed for 25 seconds, flew right, brought up droppings.

11:32 Male flew in from below, stood on rock for about 3, 4 seconds, fed for 19 seconds, flew down to cauldron.

11:47 Female came in from below for 13 seconds, fed for about 30 seconds, then incubated young for 5 minutes 50 seconds, then flew left.

12:55 Parents had a break in feeding, female came in with a warning call, went into nest and fed, then came out and then back in and stayed to incubate chick in nest.

13:31 Male came in, wanted to feed, saw female in the nest, she signalled to him that she did not want him to feed because she was sitting in the nest warming the young, so the male did not feed and flew away.

13:32 Female flew out of the nest, carried droppings to the right, young was well warmed, breathing heavily.

A chick 10 days old, nesting care by parents on a sunny day

Chopok, July 12th, 1988

08:57 Female fed for about 5 seconds, came from below and flew away.

09:05 Female returned, walked from right to above.

09:12 Female fed for 4 seconds, then came out to the left.

09:26 Female walked for 6 seconds, fed for 5 seconds, sat on a rock and flew off to the left, but remained nearby.

09:28 Female walked around nest, cleaned her feathers twice for 3 seconds each but did not feed nestling until 10:37.

10:37 Female flew away to the left.

11:29 Female came to feed, brought droppings up, Interruption of observation.

13:50 Start of observation.

14:10 Female feeding.

14:15 Male feeding.

14:25 Female active in mating attempt with male.

14:35 Mating.

15:10 Female feeding young.

15:20 Female feeding again.

One chick just before leaving the nest at the age of 12 days, alternation of heavy rain and sunny evening weather, beginning of independent roosting of the chick

Chopok, July 14th, 1988

17:00 It is raining hard; the front is coming.

17:05 Female feeding for 5 - 6 seconds.

17:17 Female feeding, male has come with her and is courting her, courtship display.

17:37 Female feeding for 5 - 6 seconds.

17:42 Female feeding chick for quite a long time, about 40 - 50 seconds, even though the chick is mature, after coming out of the nest, mating attempt with male and flying away.

17:58 Feeding the chick for about 20 seconds, she stayed with the chick for quite a long time due to the heavy rain, during this rain she had quite a serious break in feeding the chick, until 19:20 when the sky cleared at 19:10, there were high clouds, overcast but nice weather.

19:20 She flew in with the male and went straight to feed, she fed for about 3-4 seconds, as soon as she saw me she flew away, the chick as soon as it hears her soft call while feeding, at that moment it starts to call intensely – „sířř“, which is the sign of a chick flying out of the nest. The chick will need this type of call when it leaves the nest.

19:40 Female has reappeared, warning call, within 10 metres, restless because she sees me, warning call, it took her up to 10 minutes to feed the young.

19:51 She fed the young for 3 - 4 seconds, then she walked around me warning for another 3 minutes.

20:00 The weather is beautiful.

20:20 She came to feed apprehensively, male came with her, until 20:22 she walked.

20:22 She fed for 4 seconds, chick always calls by sířř, female flew out.

20:22 - 20:24 Female walked with flapping wings, male active to mate, alpha male followed her, sang once, third beta male flew to her, female active again to mate, then they disappeared up to summit of Chopok.

20:39 Male and female appeared, male flew to a high place and sang, female walked slowly to the chick, fed slowly for 3-4 seconds, then walked to the left about 3 metres, male flew to the female, when the chicks leave the nest and only the female starts to feed them, the sexes are very active in the next mating, the female often being more active.

21:00 Male singing on Chopok, it is getting dark.

21:13 Female fed her young for the last time during the day, she sang a warning on the top of Chopok, after 21:20 all alpine birds became quiet.

Nesting female with chick 13 days old, chick leaving the nest, polygynadic family mix and mating, morning awakening

Chopok, July 15th, 1988

04:28 First morning song, beta male, main alpha male below.

04:32 Beta male sang for the second time.

04:36 Six more accentors came out, gathered on the top of Chopok.

04:30 - 04:40 Chick woke up, hungry and calling vigorously (sířř).

04:40 Chick first four seconds fed by the female, then coaxed out of the nest by the female and was able to immediately glide passively for about 5 metres. Next attempt to fly and glide was at a distance of 2-3 metres, could not land well yet, the female coaxed it by softly "murmuring", the chick was still calling, hungry, and so the female led the fledgeling out of the nest.

04:47 The female walked around the nesting hole, but the chick was already outside the nest, it started sucking, heard her, the female came to the chick and fed for 5 seconds, this indicates that immediately following departure the nest, vocal contact between mother and chick is very important.

04:47 The chick followed the mother to the cauldron.

04:52 She fed it again lower down in the cauldron.

04:53 The male came from below, cleaned himself a bit and flew down.

04:54 Female and male down below gathering alongside the chick, the chick moving behind them.

05:00 Female feeding for 3 - 4 seconds.

05:00 Sunrise, cold winds from below.

05:02 Two more adults, at least one, male, flew to the pairs with young, when they wanted to mate they all flew to the left and new two flew back.

05:03 Female again displayed anus to the male and the male courted.

05:05 Female collected food for 2 minutes and then fed the chick for 4 - 5 seconds, chick still called.

05:10 First call of the water pipit *Anthus spinoletta*.

05:12 Female accentor feeding.

05:13 Female feeds young for 4 - 5 seconds, the young are sitting quieter.

05:14 Female walks around and calls warningly.

05:14 A second part of the family flew to these birds from the bottom towards Chopok summit and then to the east, but they did not collect insects.

05:15 Birds are chasing, adults were accompanied by three young, the young were already flying well and even sharply with steep turns.

05:20 Two of the juveniles from the arriving group were cleaning up.

05:25 Male sat looking at the newly-fledged chick of the female newly arrived from Chopok.

05:28 The female fed the fledgling for two seconds, she came with the call carefully and left carefully, the chick has stopped changing place, the early morning has become the most important time of day; when the female moves the chick from one place to another with the call because the chick is hungry, later, as the chick starts to be fed, it stops changing place and is more quiet, which is safer.

05:32 Two adults from the bottom group, (which had the three young) moved from the bottom to the top of Chopok, the male was singing, their juveniles were flying shorter distances upwards, their tails were fully grown and they were already actively searching for food on their own.

05:40 The bottom group appeared again on the top of Chopok, one of the young sat for 30 seconds and then flew behind the adults, undoubtedly such young fly also behind the adult male, (i.e., the male guides them but does not feed them).

05:48 One of the adults of the lower family is cleaning itself.

05:55 In a pair with a single chick, the female moved to feed the fledgling, the male sat higher up, did not feed young.

05:57 Female fed for 2 - 3 seconds, male sang higher while doing so, female sat about 2 meters next to fledgling, called warningly and then flew away.

06:14 Both parents arrived, only female feeding young, male courting.

06:20 Female collected insect.

06:21 Female was preening near to fledgling.

06:22 Both, female and young sitting.

06:40 No more calling from the second group of accentors.

06:59 - 07:00 The female was preening, sitting close to fledgling.

07:12 She came, but only with a soft warning call.

07:15 Female flew away for a few metres, resting, soft warning call.

07:16 Female standing on alert.

07:27 - 07:32 Alpha male cleaning.

07:32 Alpha standing on alert.

07:34 - 07:38 Alpha preening for about 20 seconds, then preened again for 10 - 20 seconds.

07:40 Alpha took off, sang, began feeding.

07:47 Alpha sang.

08:10 Female arrived, wanted to feed young in the original crevice where it was at 06:14, fledgling not heard from new location, female did not find it, flew away, arrived at 09:00.

09:14 Alpha male cleaning, female feeding fledgling.

Feeding during intense onset of feather growth in nestlings in a large family, nestlings at 5.5, 6, 7, 7 days of age, role of females in a polygynandric family

Konský Grůň, July 9th, 1988

The clouds are at the level of 2000 m, on the top of Chopok, therefore the upper nest on Chopok was in worse conditions than the lower nest on Konský Grůň, but together it was one polygynandric family, where the lower nest on Konský Grůň had produced young earlier than the nest on Chopok. It was likely that the females that raised chicks at lower elevation were more experienced, as on Konský Grůň they nested in the same rocky nesting hole as in the previous years and the hole is selected by the female. They nested earlier than the females from the higher elevation. Thus, females from lower located nests bred in better conditions than the upper females and were more experienced than females from the summit. Breeding success of females from lower nests was higher than females from upper nests.

14:01 "Lower female": Female came from the left, did not notice people on the hiking trail at all, jumped on a rock and fed briefly, walked higher up on the ridge, came to the nest while feeding with a quiet warning call, young very intense called in the nest and could be heard up the trail.

14:09 Alpha male came from above, fed quickly and flew off to the left.

14:10 Female came to the nest, fed for 5 seconds, flew off with droppings to the left and dropped the

droppings in flight after about 10 meters on the ground (important for protection from predators).

14:15 Female came in from left, went in, fed for 10 seconds, showed herself in the opening, came out, picked up droppings and flew out left after about 18 seconds in total.

14:27 Again the female came to the nest for about 120 seconds, then flew over to the rock, fed for 7 seconds, came out on the ridge above the nest, sat on the rock and watched for 20 seconds, then flew up towards the cable car.

14:30 Female flew down to the rock, went to the nest for about 30 seconds, fed for 7 seconds and flew left towards the cable car.

14:35 Flew again from below the lifts for about 2 minutes, walked around the nest warning, fed for 4 seconds, then flew out and cleaned her feathers for 30 seconds, stimulated by the heat and sun.

14:45 Alpha male appeared, approached the nest for about 40 seconds, fed for about 4 seconds, left the nest about 30 cm away, sat there for 30 seconds and then flew down into the cauldron.

14:47 Female came in, went to the nest for about 60 seconds, fed for 5 seconds, came out but went back to the nest, sat down for about 7 seconds and then flew out to the left.

14:57 Arrived on rock for about 30 seconds, fed young in nest for 7 seconds, returned to nest for 8 seconds, then flew left under cable car (heavy tourist traffic).

14:58 Alpha male came directly behind her, fed for 10 seconds and flew off to the left with her.

Intensity of evening mating

Konské, July 11th, 1991

Intense evening mating between 18:30 and 20:45, the male sings and the female flaps her wings about five times near the male, attracting the male for copulation.

Distribution of food to chicks in the nest, 10, 10, 10, 11 days old chicks. Experiment

Chopok, July 12th, 1991

18:05 Female fed, had 4 young in the nest.

18:15 Female fed young, nestlings were experimentally marked and divided into front, left, right and back. Front got 2x, right and left 1x, back not once. She brought 7 tipulids.

18:22 Sunny, sun even on the nest, she fed, brought 3 tipulids, front got 2x, back once.

18:32 5 tipulids in beak, female feeding (no doubt she has extra food in the crop), back was fed 4x, front 3x, left 3x, right got nothing.

18:55 Alpha male and female cautiously went to nest, warned together, saw some danger, but it wasn't me, only fed at 19:18, left one got 3x, right one 1x, front one 1x, back one 3x, picked up droppings, next to the young the alpha male collected insect and warned.

19:30 Alpha male fed, 1x in front, 1x left, 1x back, right got nothing, after feeding he flew out and sang about 3 metres from the nest.

19:54 From 18:15 to 19:54 the front young was fed 9 times, the back young 9 times, the right one

only 2 times, the left one 8 times. The chicks were marked experimentally, the front one was moved backwards, the back one forwards, the left one to the right, the right one to the left. By experimental relocation of the chicks in the nest it was determined on the next day whether they would return to their original position.

20:00 The female fed, breeding behaviour of adults was not interrupted by the experiment.

Relocation of nestlings after the experiment, 11, 11, 11, 12 days old chicks

Chopok, July 13th, 1991

14:35 The nest was inspected after the storm, the chicks rearranged during the day, the back (formerly front) chick moved back to the front, the right (formerly left) chick moved back to the left, the back chick that was transmitted forward took the position of the right chick, and the chick that was probably the weakest fed the day before moved to the back. It is very likely that the parents stimulate the chicks to move in the nest by the frequency with which they feed each chick, so that there is only a few hours' difference in the development of the chicks in the nest.

Increasing male feeding intensity before chicks fledge, the need to leave the nest quickly and reduce the risk of breeding extinction by dispersal of chicks, chicks before fledging at 12, 12, 12, 13 days of age

Chopok, July 14th, 1991

10:05 Male feeding, 3 tipulids (Crane flies).

10:15 Male, one crane fly sticking out of beak (it was after a storm and tipulids are easy to collect).

11:05 Female fed, 3 tipulids.

11:12 Male fed, 3 tipulids in beak.

11:26 Male feeding at least 3 tipulids.

11:29 Male, 3 tipulids.

11:41 Male, 3 tipulids.

11:47 Male, 3 tipulids.

Pre-fledging position of the chicks in the nest: back (12/7) - front right today - partially out of the nest, front (12/7) - front left today, right (12/7 was least fed) stayed back today, left (12/7) out of the nest today. The position of the weakest chick was maintained until it fledged.

Post-nesting care, female, fledglings, care for passively flying juveniles, young 15, 16 days old

Between Nový and Havran, Belianske Tatras, July 8th, 1991

Family about 4 - 5 individuals.

12:15 Female fed young about every half hour, male is near and feeds only himself.

13:15 The female and male tend to mate when they come to feed. When the female is in search of food for her young, she may not be as interested in mating with the male. Therefore, males will take advantage of the time when the female is feeding her young and can spend some time with them.

14:00 Female arrived to feed fledglings.
 14:05 Male came attracted by the female.
 14:07 The male stands close to the female.
 14:09 Male stands close to one juvenile. Males no longer feed the fledglings, but they are important to them, because the juveniles often fly after them and learn to get to know their surroundings.

Care for actively and well flying juveniles

Nose below Slavkovský summit, eastern slope, August 14th, 1992

Young active and fly well, both associated together, only the female feeds them, the male is mostly absent, he appears rarely.

Discussion to frequency of nestling feeding

On the mountain tops of the French Pyrénées, Alpine accentors built nest in rock and turf crevices, on shallow slopes or steep cliffs. A male, alpha, often accompanied the female while she collected nest material, but he never helped (Davies *et al.* 1995). A male helped a female with nestling - feeding only if he gained more than a critical share of the matings with her (Hartley *et al.* 1995). Males clearly preferred to compete for matings rather than help with parental care, so if a female's nestling period overlapped the fertile period of another female, she was much less likely to get help. Most females gained some male help. On average, males brought 22% of the feeds 5-day-old chicks were fed approximately 4 times per hour by females and 2 times per hour by males, 12-day-old nestlings were fed approximately 7 times per hour by females and 3 times per hour by males (Davies *et al.* 1995). When females were assisted by only one alpha male, the alpha reduced the amount of assistance it provided as mating percentage decreased. This arised when alpha males had opportunities to mate with other females (Davies *et al.* 1996).

From the observations presented above, it is clear that the amount of feeding of the chicks depends on the number and the age of the chicks in the nest, on the current weather conditions, as well as on the specific hour of the day. In the case of the 7-day-old nestling that was alone in the nest, the female fed 4 to 5 times per hour in the afternoon, and the alpha fed once or twice per hour. However, if there were four such nestlings in the nest, the female fed them up to eight times per hour in the afternoon. The alpha fed them at least three times. Heer (1996) reported from the Swiss Alps that chicks in the second half of the incubation period were fed in the morning with an average interval of 12 minutes (6 times per hour). Females contributed about 65% of feeding, alpha 15 and beta 5 (Heer 1998). Dyrz (1976) reported from the Giant Mountains that 11-day-old chicks were fed 7 to 9 times per hour in the morning, the intensity of feeding decreased between 3 p.m. and 8 p.m. (5 to 6 times per hour), and increased again in the evening. In one nest the female provided

79% of the food and the male only 11%, but in the other nest the female provided only 30%, the alpha 35% and the beta 10%. The other foraging adults were not identified. So the female plays a key role in nest care, even though there may be more male helpers at the nest.

Commentary on the breeding to moulting period and its role in the transmission of ectoparasites

Alpine birds are adapted to live in cold environments in many ways. The Alpine accentor is a true representative of the alpine ecosystem, highly adapted to harsh environmental conditions. In the High Tatras, snow cover lasts for almost 7 - 8 months of the year. Temporary snow cover is not uncommon even in July and August (Fig. 1a). Alpine accentors return from wintering grounds in March and April. They begin breeding towards the end of May. Nesting usually continues until the end of July (Fig. 1b). After the nestling period, parental care is reduced in males. Fledglings are mainly cared for by females. This enables males to begin molting earlier than females but almost all accentors have finished moulting by the end of September (Haas and Janiga 2020). If there is any overlap between breeding and moult, it is in females about this time. The possibility of horizontal transmission of ectoparasites between adults during nesting and incubating eggs or hatchlings was mentioned above. This is the period (May - June) when the greatest variability in the different activities of the birds occurs (Fig. 1c) and when the ectoparasites begin to change their population strategy. This change is also accompanied by a change in the morphology of the lice or mites (Figs. 1d, 1e). For example, regular moult in Alpine accentors has also an effect on seasonal population dynamics of louse *Philopterus emiliae*. In September, during moult, the numbers of lice increase, and the body of the adult lice gets smaller. This may be as an adaptation to avoid preening by birds, which is more frequent preening during moult than at other times (Moyer *et al.* 2002). More frequent preening in daily cycle of Alpine accentors during moult than during breeding was also observed by Janiga and Romanová (1997). On the contrary, during the winter period, preening is much reduced and new feathers after moult offer favourable conditions for feather-eating lice, thus their number and size increase (Janiga and Kubašková 2000; Janiga and Mičková 2004). Winter is the most convenient time for these ectoparasites (Janiga 2018), but a demanding period for the birds. Seasonal prevalence of bacteria in Alpine accentors may indicate these energetically demanding periods in annual cycle of the birds, when the birds are weakened and more prone to infection. Two highest peaks of *Klebsiella*, *Yersinia*, *Staphylococcus*, *Bacillus*, *Pseudomonas*, and *Pantoea* prevalence occur in winter and early spring (Fig. 1f), and then the end of the moult period (Janiga *et al.* 2006). Moult in Alpine accentors has also important role in life cycle of the ectosymbiotic feather mite *Proctophyllodes megaphyllus*. In contrast with louse *P. emiliae*, the male mites are largest in autumn

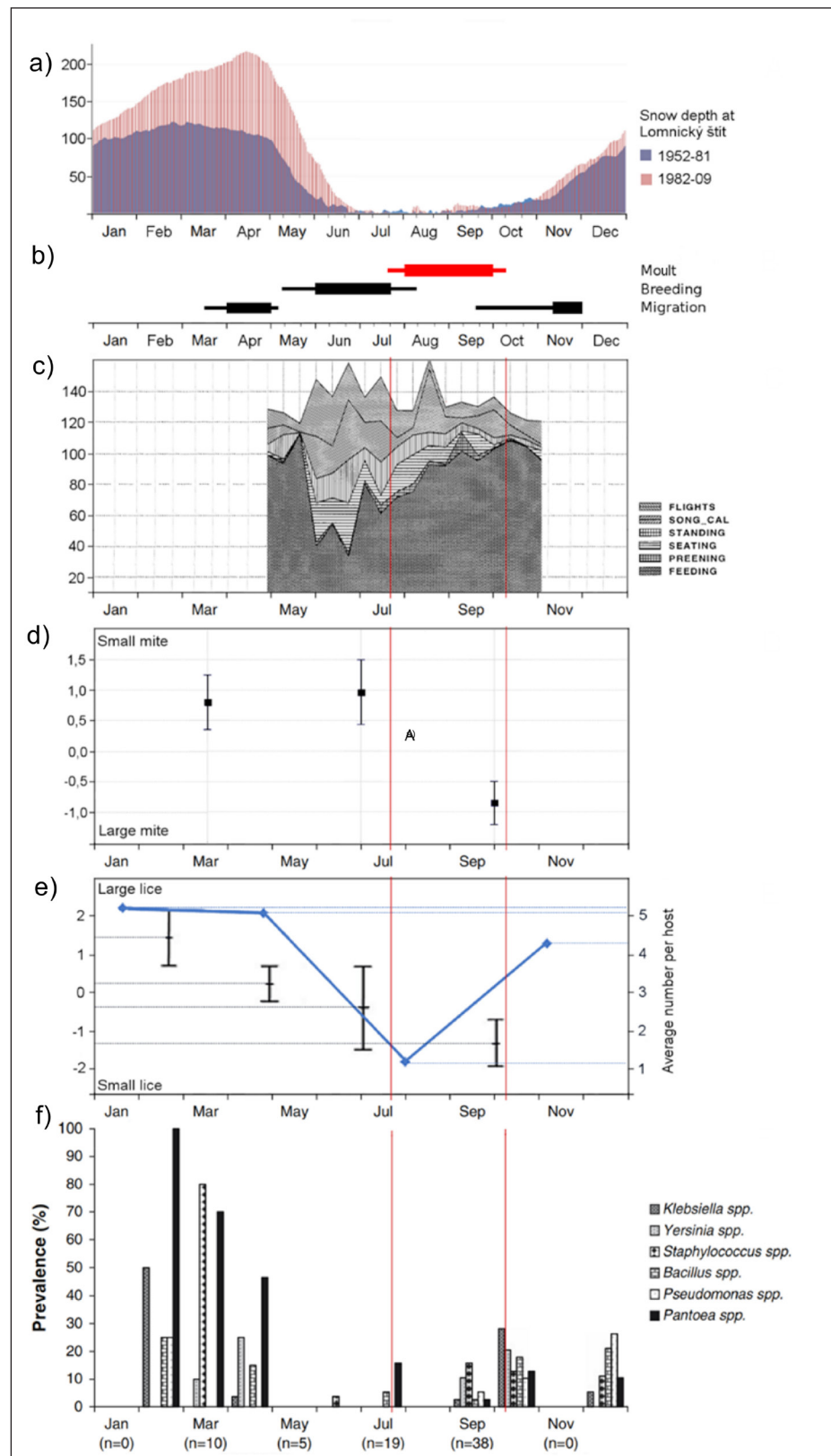


Fig. 1. Compilation of various factors in the annual cycle of Alpine accentor. a) annual course of snow depth (cm) at peak Lomnický štít, 2634 m a.s.l., two successive averaging periods (Vojtek 2010). b) moulting - thin lines show possible but not common moulting periods; breeding - thin lines include prebreeding activities and fledgling period; migration - thin line during the spring represents migration, thick line arrival to the breeding sites. Thin line during autumn represents formation of aggregations and thick line definitive leaving to the breeding sites (Janiga 2023). c) seasonal variation (in %) in the main activities of Alpine accentors in The Tatra Mountains (Janiga and Romanová 1997). d) difference in size among seasons in male *Proctophylodes megaphyllus*. Principal component scores reflecting size with their 0.95 confidence limits (Marčanová 2020). e) size of the adult lice *Philopterus emiliae* from Alpine accentors in different seasons. Left Y axis - means of principal component scores with intervals of standard errors (Janiga 2018). Right Y axis - blue line, average number of *Philopterus* lice per one host (Janiga and Mičková 2004). f) seasonality of occurrence of bacteria identified in faecal, cloacal, and pharyngeal samples from Alpine accentors, genera with low occurrence in summer (Janiga *et al.* 2006).



Fig. 2. Left: Alpine accentor, June 8th, before moult, the plumage is worn. Note the abraded white tips on coverts and feather edges. Right: Alpine accentor, October 6th, plumage fresh after having been moulted. The feathers have a sharper outline and a darker colour (Photo: F. Korec, 2021).

(Marčanová 2020). Newly coated feathers (Fig. 2) represent favourable food opportunity for the mites and also birds do not seem to remove them actively during the preening unlike parasitic lice (Blanco *et al.* 1997). Therefore, moult may be advantageous stage in mites' year cycle. Although, lice and mites share similar environmental conditions in the hosts feathers, they both must follow the annual pattern in moult of the Alpine accentor (Marčanová 2020), which has ecological impact on these parasites.

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