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Biology of alpine accentor (*Prunella collaris*) VIII. Growth and postnatal development

M. JANIGA

Institute of High Mountain Biology, Žilina University, Tatranská Javorina 7, SK-059 56, Slovak Republic; e-mail: janiga@uniza.sk

Abstract. 62 measurements of 91 nestlings and juveniles of *Prunella collaris* were taken in the High and Low Tatras (Western Carpathians). Growth curves of head, bill, hind limbs, forelimbs, primaries, rectrices, as well as total wing and body weight were described. The strong isometry between the tarsometatarsal and antebrachial skeletons and the rapid growth of the wing bones in the first half of nestling development should be correlated with the intensity of activities involving the fore and hind limbs. The hind limbs of birds are not only responsible for supporting the body and moving about on the ground, but also play a key role in flight during take-off and landing. The bones of the legs are subjected to axial, bending, and torsional loads. Accentors do not show a typical sigmoidal curve in weight gain like some other altricial species. Particularly in the first few days after hatching, weight gain is high, indicating a short-term presence of chicks in the nest. Hatchlings grow at about the same rate during the first half of the nestling period, and later, hatched nestlings grow at about the same rate as their older siblings, only lagging in development at the time of hatching. During the second half of the nestling period, the rate of feather growth relative to weight is higher in younger chicks than in older chicks. In older chicks, feather growth slows as the weight of the internal organs increases, so that by the time the nestlings leave the nest, younger and older siblings are already at approximately the same developmental level. This is achieved over a period of two or three days as the chicks move around under rocks.

Key words: Alpine accentor, *Prunella collaris,* growth and development, skeletal, body weight and feather growth trajectories

Introduction

Nestling growth studies can yield insight into the effects of different nesting strategies on productivity of birds (O'Connor 1984), as well as the impacts of parental effort and environmental variables on fitness (Ricklefs and Peters 1981; Magrath 1991). The short period young spend developing in the nest is a critical part of a bird's life cycle and a nestling's developmental path can affect its survival to independence, its survival as an adult, and its future reproductive success (Bolotnikov *et al.* 1985).

A major question in evolutionary biology is why life-history traits vary among species (Charnov 1993). Attention has focused on traits such as fecundity, age at first reproduction, survival, and rate of aging. Growth and developmental rates have received less attention even though they are integral components of life-history strategies and vary widely among species (O´Connor 1984). Several factors have been hypothesized to influence evolution of growth and developmental rates in birds (Starck and Ricklefs 1998). Some factors associated with species-specific growth-rates and patterns include nest location, synchronicity of hatching, and brood size. Ecological factors that influence nestling growth are related to limitations of food availability, microclimate, habitat differences, parasites, intraspecific competition, and parental abilities (O´Connor 1984; Davies 1992; Ricklefs 1993). Predation has a strong influence on the growth of altricial bird species along with significant contributing effects including foraging mode and clutch size as well as other developmental strategies like clutch adjustment, brood reduction, and hatching asynchrony (Janiga 1992a, b; Remeš and Martin 2002). These factors confirm that evolution of growth and development of altricial birds are shaped by extrinsic environmental forces (Janiga 2005a). Species with higher nest predation fledge at a lighter relative mass (Remeš and Martin 2002).

The aim of this study is to summarize current knowledge on the growth and development of nestlings and fledglings of alpine accentors in relation to the necessity of their adaptation to the short growing season in high mountain habitats.

Material and Methods

Research on *Prunella collaris* has been ongoing. The first data on this bird species were systematically collected in 1984, and research continues to this day. Hatch date and sibling order were recorded from six nests at the first visit after the chicks hatched; the hatch date was marked as day zero. Once nests were found, they were visited regularly at two-day intervals throughout the incubation period. From the measurements of nestlings, primary growth curves of each organ were determined in relation to the chronological age of the birds. The most accurate nestling age would result from checking a nest daily, but this could cause stress on the birds and can lead to increased predation. The ages of chicks found in additional nests were determined from the primary curves obtained in the initial six nests. In total, 20 nests were visited. Data from measurements of 65 nestlings and 26 actively flying juveniles studied between 1988 and 2023 in the High Tatra and Low Tatra Mountains (Slovakia; Western Carpathians) are used in this study. Birds were found in a nest or captured using ornithological claptraps or mist nets (Fig. 1). Each individual was measured to the nearest 0.5 mm using calipers and weighed to the nearest 0.1 g using a Pesola spring balance. Nestlings were uniquely marked with a felt-tipped pen, and older nestlings were ringed with a combination of coloured plastic rings so that each individual could be identified. A total of 162 comprehensive measurements of nestlings and juveniles were carried out.

Fig. 1. Preparing mist nets in high mountain environments in rocky valleys. (Photo: M. Janiga, 1988).

Measurements included

Tarsometatarsus length (base of the middle toe - middle of the fifth joint below the caudaloventral region of the edge of the lateral tubercle of the tibiotarsal trochlea), antebrachial skeleton (area of the ulnar process / olecranon - carpal region at the site of the articular surface of the radiocarpal joint), head length (area of the occipital bone - tip of the bill), head width (point between the right and left zygomatic arch), beak width (distance between the right and left fleshy areas at the base of the bill where the upper and lower mandibles meet, often enlarged in young birds), and beak length (one jaw at the tip of the upper mandible and the other at the base of the bill where it joins the skull - culmen). The longest primary was measured from the point where the fleshy sheath emerges from the skin to the tip of the feather, the primary vane was measured from the superior umbilicus to the tip of the feather. Tail length - from the insertion of the middle retrix to the tip of the longest retrix.

Data were plotted using the distance weight least squares method, the STATISTICA 12 software (Stat Soft CR, Prague, Czech Republic).

Results and Discussion

Patterns of behavioural, morphological and sense development

Altricial birds show low pronounced imprinting after hatching since they have several days to recognize the characteristics of the birds feeding them. In accentors, maternal recognition is essential once birds leave the nest because they are dependent on her for subsequent support. In altricial species this initial stage is devoted to postnatal growth, and during this period the sole task of a nestling is to ingest food presented to it and convert it into its own biomass with high efficiency. In this study, several categories of behaviour of the altricial young are catalogued by time of their appearance:

Day 0 – 1: Eyes closed. No pins are visible below skin. Down is present on the capital, humeral, dorsal, alar, crural, and ventral tracts and is greyish black. Vertical gaping; the gape can grow quickly early in the nestling period. However, the rictus - soft tissue at base of bill - is very pliable during growth, and measurements of the gape can increase or decrease between days as the rictus contracts and expands.

Day 2: Down on forehead, neck, back, shoulders. Eyes still closed. Alar pins have grown towards posterior edge of wing – 2 mm, The rictus is big in relation to size of the head. Chicks can weakly lift forelimbs. Shifting on tarsi, voice a distinctive weak twitter.

Day 3: Alar pins have grown towards posterior edge of wing and in some individuals may be pushing out of skin. Other characteristics are consistent with the second day. Egg tooth is still visible in some chicks.

Day 4: Alar pins have emerged – 0.5 mm, tail pins visible, eyes begin to open but do not see, full lifting of forelimbs, well shift on tarsi.

Day 5: Strong twitters or quiet „tschib", leading to predation of two birds from a single nest, Alar primary, secondary and tail pins have emerged, well shift on tarsi, voice good, begin to see through eye slits.

Day 6: Primaries and secondaries still in quills, primaries 10 mm long on average (Fig. 10), in some individuals the primaries begin to unsheathe, pharynx vermilion with two black spots in the center, gape – whitish red, eyes open approximately 80%.

Day 7: Better movement with wings, already spreads both when moving on tarsi, squeaks well, eyes open, Ventral tract is not yet fully covered with feathers, Primary vanes 2-3 mm (Fig. 10).

Day 8: Young can move well, good wing movement, ventral tract not yet fully covered with feathers. Eyes open, feathers on upper body are better developed than on underparts. Vanes of primaries 3-5 mm long, primaries on average 20 mm long (Fig. 2).

Fig. 2. An 8-day old nestling, July 10th, 1988, Chopok, Low Tatras. At this age, the chicks are already moving on their tarsi, using their wings to help them move. They do not have stable thermoregulation, so the mother keeps them warm in the nest if necessary. (Photo: M. Janiga).

Day 9: The chicks were already able to move to dry places outside the nest if the nest was covered with snow or flooded. Down still on the sides of the head. Upper parts of wing better covered by feathers than underparts, vanes of primaries approximately 6-9 mm long, feather tracts of tail start unsheathing, shifts on tarsi with vigorous wing movement.

Day 10: Body feathers are well developed but tibia and femur are still weakly overgrown with feathers. The tibia and femur are still lightly feathered, a key period of allometry when weight rates are reduced at the expense of significant feather growth (Fig. 8). Down is still present on the sides of the head. Underparts of antebrachial skeleton are well covered by feathers, underpart of ulna/radius is not yet well covered. Two juveniles of this age in one nest were found with a broken tarsus, underdeveloped, suggesting genetic variation of weak bone during tarsal development. Ventral tract not yet fully covered with feathers.

Day 11: All feather tracts continue to unsheathe extensively. Primaries are unsheathed about 15-20 mm. Still remnants of down on the sides of the head. Legs not yet fully feathered, cools with beak open in warm weather. Noticeable change in the voice from squeaks to "síí" calls. Ventral part completely overgrown by feathers. The underpart of wing is also completely covered with feathers. The caudal tract is not yet fully feathered.

Day 12: Primaries reaching a length of about 45 mm. Tail feathers 30-32 mm long (Fig. 10). Still reduced increments in the body weight (Fig. 8). Actively calling adults „síí ". The rictus on bill still developed.

Day 13: Legs fully developed, self-roosting, thermoregulation complete, passive gliding, bills of some individuals are already darkening, some still have well developed rictus. Many chicks infested with lice and mites. Underparts of wings completely covered with feathers. The developmental lag of the younger individuals in the nest is reduced, the younger ones are catching up with their older siblings (Fig. 14). At this age, the chicks leave the nest and begin to walk and hide under rocks (Fig. 3).

Fig. 3. A 13-day old chick, immediately after leaving the nest. On the thirteenth day the chicks leave the nest and are usually seen within 10 metres from the nest. They roost alone, (i.e. they have their own thermoregulation). They are actively fed by their mother, who often entices them to change their hiding place by feeding, as the young are very vocal („síí" calls) when hungry, especially in the morning and evening. They fly passively (glide) to escape from danger but can also turn to a chosen spot in flight. In the event of imminent danger, they open their red beak wide inside, which they probably use as a moment of surprise in front of predators. July 15th, 1988, Chopok, Low Tatras. (Photo: M. Janiga).

Day 14: All feather tracts are significantly unsheathed, giving young an overall feathered appearance. At this age the young fly poorly, but quickly run under rocks, their beak begins to darken from the outer and inner part, many of them are infested with lice and mites. Young birds become increasingly hungry and at this age gradually mimic adult feeding behaviour or they may try, usually unsuccessfully, to take a food item from the ground.

Day 15: At this age, the young still walk rather than fly after the female. The rictus is disappearing. Some individuals are already capable of active flight to the mother. The birds are fully feathered. Atrophy of the thigh and calf muscles has been found in some individuals.

Day 16: Chicks start following the mother. The females are primary caregivers, very rarely helped by males. Currently, young birds show a progressive tendency toward flocking, and seek other accentors. They can fly over lakes or actively climb hills. The ventral part is not yet brick red, but grey, and the wings are coloured brown. The rictus has already disappeared in all animals of this age. The chicks no longer call "síí"; the voice is mutating. At this age the voice begin to break, resulting in soft, half-voiced song.

Day 17: Juveniles feed independently on grass seeds and various species of larger insects (Homoptera), they discard undigested food. Excrements can be up to 10 mm long and several millimetres wide, for example cocoon remains, legs or chitinous insect parts. Adults make an imperfect call or 'half-voiced song'. Primaries are quite worn when moving between rocks. The belly is not yet cinnamon buff, there are brownish-white spots on the tectrices.

Day 18: They feed themselves, but when they see the mother, they ask for food. The mother feeds them sparingly. Spots on the wings already developed, beginning of juvenile molting - especially some secondaries and wing coverts. Forehead, crown, hindneck, and sides of head and neck are dull grey with a brown tinge to the feather-tips. The feathers are finer, browner, and less streaked. Mantle, scapulars and back to the part of the tail tail-coverts are streaked cinnamon-buff and black or blackish brown. The rump and upper-tail coverts are less distinctly streaked. They can already drive some other bird species away from food (*Anthus spinoletta*).

Independent juveniles, those not being fed by mother, still associate with her, and 5-week-old birds may be seen following a parent. Older juveniles form small flocks of juveniles and adults, often visit mountain peaks or huts where they may learn a synanthropic way of life. The first adult feathers are adult-like, but often retain the juvenile tail, flight feathers, primary or tail coverts (cf. the same in Witherby 1940). The beak is already yellow, black (Fig. 4), the inside of the beak is no longer red, the eye is brown, and many birds are still mutating. The juveniles are increasing in weight and wing length, they are still growing (Fig. 15). Juvenile flight plays occur from day 21 of age, peaking on day 30 after hatching and lasting until day 40 of age (Glutz von Blotzheim and Bauer 1988). Young change their plumage in August (Mauersberger *et al.* 1974). In the Nepalese Everest region, where the alpine accentor is common at altitudes around 5 000 metres, juveniles begun to molt in the third week of August, and the moult of is completed by the end of September (Diesselhorst 1968). In the Alps (Bub 1984), or Carpathians (pers. obs.), young birds are also finished moulted in September. If wing coverts are only partially renewed or not renewed at all, this should be noticeable on the living bird (cf. Whiterby 1940).

The mouth is one of the first structures used by a young bird. In alpine accentors, culmen length and gape width increase rapidly between day 0 and day 8 (Fig. 5). In this species, the initial growth of the bill is faster during this early period than it is later in nestling life. The gape initially widens until day 8 post-hatch. In older nestlings, the gape gradually narrows as the fleshy rictal parts of the mouth harden. These changes in mouth size serve to allow an increase in food size and to alter the shape of the mouth, which initially serve as a feeding target for adults seeking to insert food into the beaks of helpless young, but later must serve the fledgling as a foraging tool. At 13th day of age, young usually leave the nest, before mastering flight. It is therefore not surprising that chicks that leave the nest

Fig. 4. Self-feeding juveniles, which are more than a month old, already have a beak coloured yellow, but the underparts under the beak are very grey, and the eye is brown. Young birds resemble adults but they are duller with unspeckled throat, brownish-grey head and chest, brown breast and flanks, buff wingbars (but less well-defined than in adults). Ďumbier, Low Tatras, July 12th 2006. (Photo: M. Janiga).

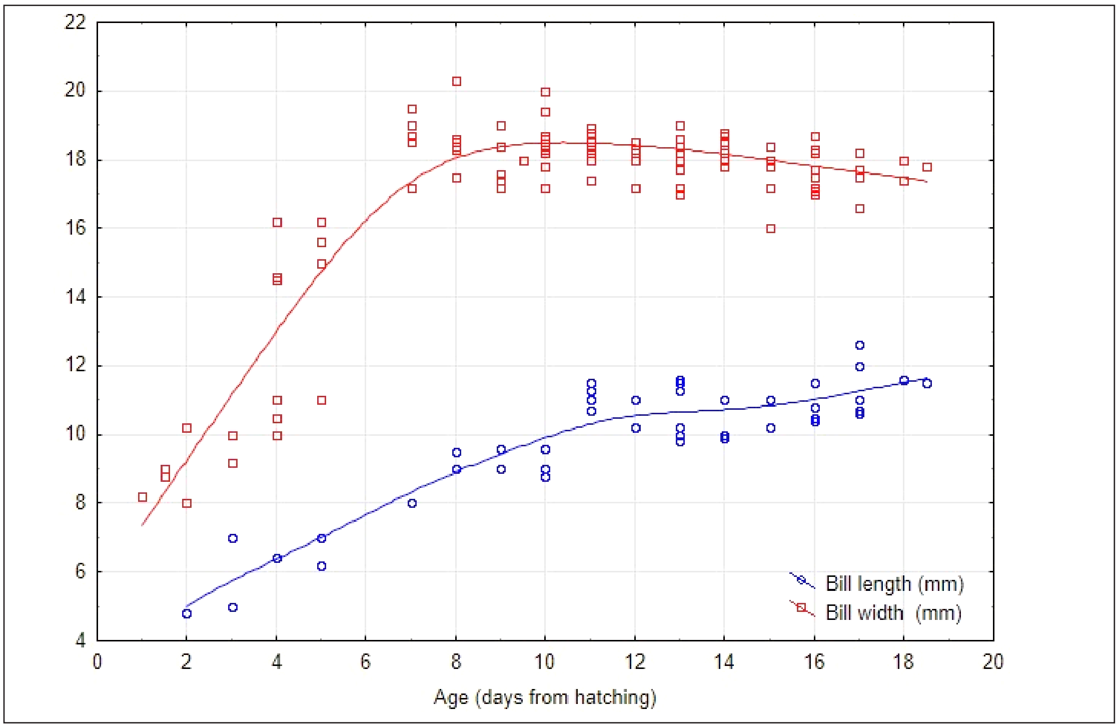

Fig. 5. Growth of the bill of the alpine accentor (the West Carpathians). In older nestlings, the gape gradually narrows a little as the fleshy rictal parts of the mouth harden.

on the thirteenth day and hide under a block or in grass still have fleshy rictal parts (Fig. 6), whereas 15 - 16-day old chicks capable of active flight already have a hard beak.

Head – cranial part

A comparison of the growth-rate between the rostral (Fig. 5) and cranial part (Fig. 7) of the skull might appear logical. In early postnatal development, growth-rates of the bill are faster than growth-rates of head. The supply (bill) organs are necessary to fulfill the nutritional demands of the growing animal, whereas the development of the demand organs (brain) can be adapted to different functional needs and quality of diet. A recent study that investigated effects of variable protein in the food of altricial young during the nestling phase, found an inverse relationship between growth of body mass during the post-fledging period and adult cognitive performance; this pattern was interpreted as demonstrating the cost of catch-up growth following a period of poor nutrition (Fisher *et al.* 2006). Cognitive performance can be associated with substantial differences in head growth during the sub-adult period. Young of altricial birds with high protein in their diet may have larger heads in proportion to tarsus or body mass than birds with lower protein levels in their diet. In cognitive performance experiments, high protein diet birds master associative learning tasks more quickly than birds reared on a diet with the low protein content (Bonaparte *et al.* 2011).

Fig. 6. The head and bill of 13-day old young. At this age, the nestlings leave the nest. (Photo: M. Janiga, 2006).

Body weight

Nestling body structure does not develop uniformly throughout the nesting period. Instead, those structures used most by nestlings whilst in the nest develop rapidly and those not functional until the birds fledge develop more slowly. Variation in postnatal development leads altricial hatchlings to differ in the degree of maturation of anatomy, physiology, and behaviour. A major determinant of growth-rate in birds is body weight. Figure 8 shows the relationship of body weight and wing length growth-rate. The growth curves reveal several points of general interest. Accentors do not show a typical sigmoidal curve in weight growth compared to some other species of altricial birds. Especially in the first few days after hatching, weight gains are already relatively high, indicating a short-lived period in the nest. In the first days after hatching, digestive organs make up a considerable proportion of the total weight of nestlings. At first, the gizzard alimentary tract, and liver grow at a greater rate than body weight. The ability of the young to process food for growth thus increases very rapidly with

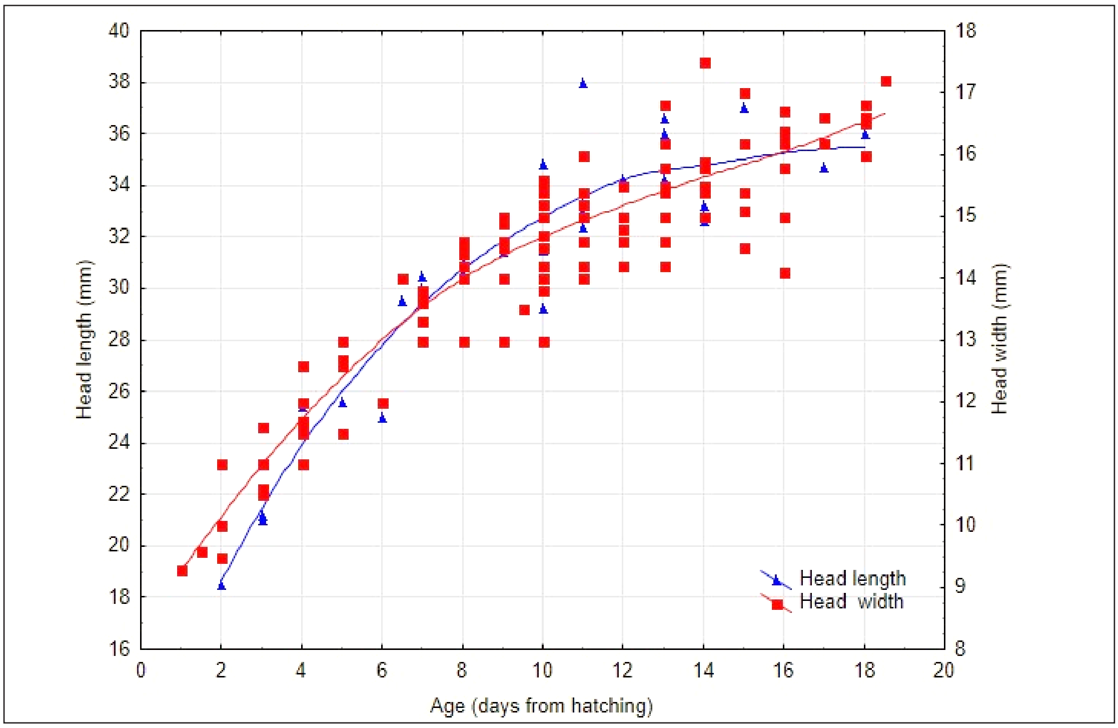

Fig. 7. Growth of the head in the alpine accentors.

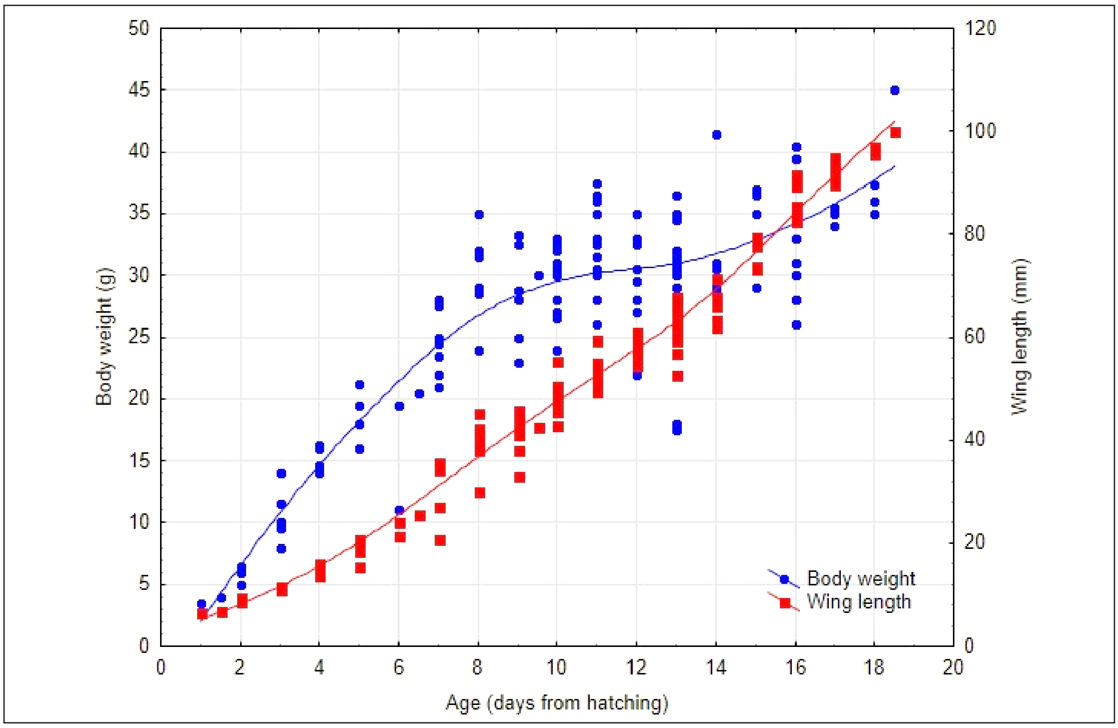

Fig. 8. Postnatal growth curves of body weight and wing length in alpine accentors. At an average age of 13 days after hatching, nestlings leave the nest.

age. At the age of nine days, the average weight of nestlings is about five to ten grams less than that of the adult female feeding them. Rapid wing growth and a slowing of weight gain after day nine of postnatal development (Fig. 8) suggest that the development of precocial functions, which were absent in hatchlings, intensifies during this period. Precocial functions include temperature regulation, ground locomotion, and flight. These three functions develop at different rates and any of them could be the source of the constraint on growth-rate. Both flight and temperature regulation require plumage development of the primaries, rectrices, and contour feathers, and the two are rarely synchronized in development. All three precocial function require the development of muscle mass. The extent to which muscles assume mature function thus represents a possible constraint on growth-rates common to all three precocial functions. Intensive growth of primaries, rectrices, and associated musculature in accentors occurs in the second half of the nesting period. Finally, accentors leave the nest whilst still increasing in weight and feather cover, completing their progress along their growth curve outside the nest (Fig. 9).

Fig. 9. A juvenile 15 days old after hatching that is already moving outside the nest. It completes its progress along its growth curves of feathers and body weight outside the nest. July 13th, 2022, Jastrabia veža, the Tatra mountains. (Photo: M. Janiga).

Feathers

Feathers develop from dermal papillae. They start to form from feather follicles, which are invaginations that start in the epidermis and go down into the dermis. The feather filament soon grows out of the follicle; this is due to cell proliferation, which is an increased number of cells as a result cell growth and division, at the follicle base. The developmental timing of feather tracts tends to follow a consistent age-related pattern within a species and is the most easily noted trait when examining nestlings. In alpine accentors, primaries begin to emerge and develop in the pin before the rectrices (Fig. 10). Rectrices usually do not begin to develop until the 4th day of age, when they proceed to grow rapidly. Feather development may proceed independently of growth in body size or mass gain (Ricklefs 1968). Flight feather growth proceeds quickly and may be affected by factors different from those that affect mass gain. As the feather grows, its spathe, to which the rachis and wanes attach, continues to form. When the spathe is complete, the calamus begins to form at the base of the spathe. The calamus is the quill of the feather, which is the lower part that remains within the pulp cavity. It is from here that the feather is fully developed and will remain so until molting occurs. The first coat of contour feathers is termed the juvenile plumage (Fig. 11).

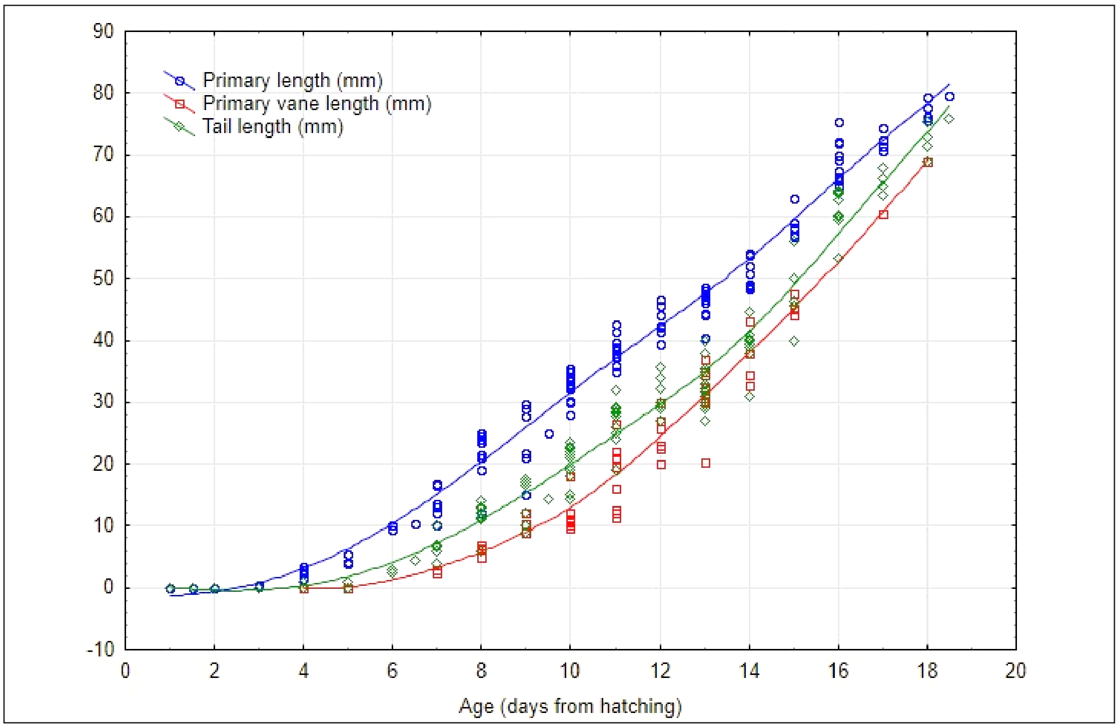

Fig. 10. Growth of body feathers in the alpine accentor.

Fig. 11. Some of the well-developed nestlings already have significantly overgrown shafts on the thirteenth day after hatching, and the underparts of the wing (carpometacarpus) are already overgrown with feathers. Primaries and secondaries are three quarters of the way out of the quills. Velická próba, Tatra mountains. July 19th, 2006. (Photo: M. Janiga).

Limbs

Chicks of altricial species hatch in a near embryonic state. They are blind, hairless, have less developed locomotor systems and depend on parental care immediately after hatching. Many comparative studies on postnatal development in altricial and semi-altricial birds have revealed heterochrony in locomotive organs. In many altricial species, the legs have a slightly higher growth-rate than the wing bones during early post-hatch development, but an equal or slower growth-rate in the second half of nest care (Janiga 1992c; Janiga 2005b; Köppl *et al.* 2005). On the other hand, in many species of songbirds with short developmental time in the nest, increments on forelimbs and hindlimbs have a linear relationship (Janiga 2005b). Alpine accentors spend a relatively short period in the nest, and are conditioned by the need to leave the nest before being capable of active flight. This shorter nesting period means that the bones of forelimbs and hindlimbs grow at approximately the same rate (Fig. 12). This kind of synchronous development of the fore and hind-limbs is associated with the establishment and improvement of distinct functions over the short nesting period. The early development of hindlimbs is a necessary concomitant of improvement in stability, begging behaviour, and escape from nest. Forelimbs are important for flying, but in alpine accentors they synchronously help the chicks move around in the nest (see above) as well as on the ground in the first days after leaving the nest. Synchronous limb growth prior to leaving the nest appears to be strongly associated with ossification, and the developmental level of forelimbs and hindlimbs is approximately the same. This means that hatchlings that the female raises from the nest can passively fly (glide) downhill about 5 m after a predator startle, but cannot yet land well, as the hind limb bones are not yet strong enough for landing. In alpine accentors, strong isometry between the tarsometatarus and the antebrachial skeleton, and the relatively fast growth of wing bones in the first half of nestling development, should be correlated with the intensity of activities involving fore- and hindlimbs. Hindlimbs of birds are not only responsible for body support and terrestrial movements, but also play a significant role in flight during landing and take-off. Leg bones experience axial, bending, and twisting loads (Casinos and Cubo 2001). This kind of shape difference may reflect different mechanical

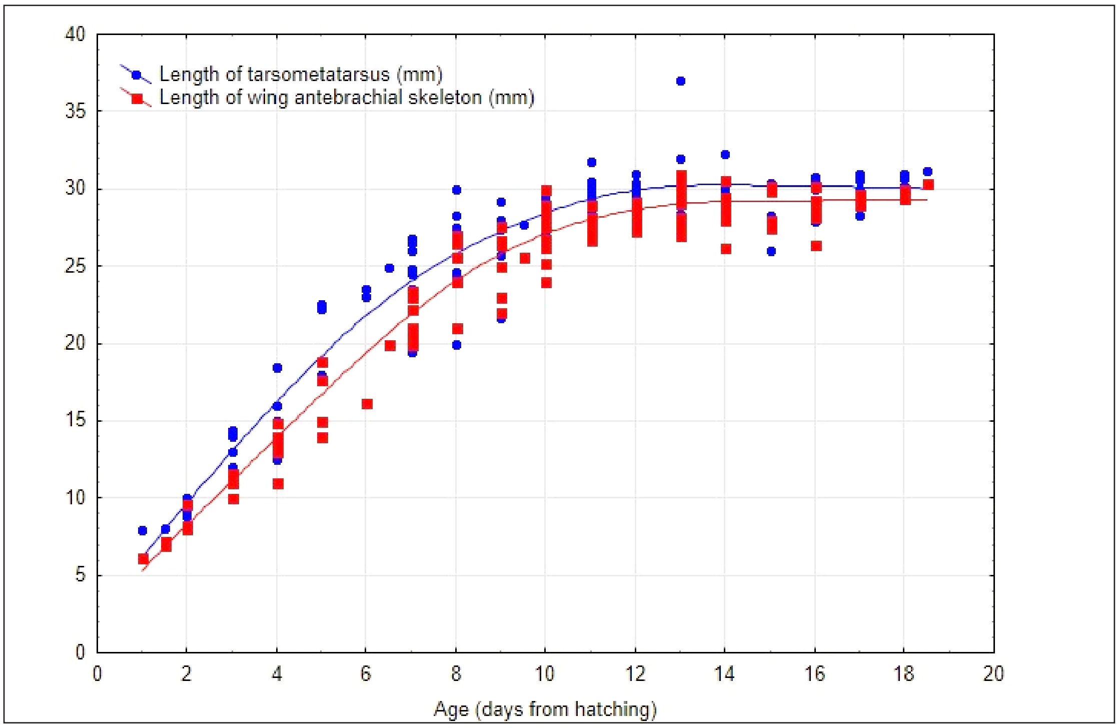

Fig. 12. Growth-rates of tarsometatarsus (hindlimbs) and antebrachial skeleton (forelimbs). Intense growth-rates in the breeding season and synchronous bone growth predict that everything in the development of alpine accentors is conditioned by rapid nest abandonment at day 13 of average age. In case of danger, young can survive even when leaving the nest at day 10 of age.

loads among hindlimb components; for example, the femur is subjected to higher torsion moments than the other limb bones (Carrano and Biewener 1999). As suggested by Hayward *et al.* (2008), bone growth-rates are determined by a complex suite of factors and interactions, many of which remain incompletely understood; furthermore, the lack of uniformity in the growth of leg bones might also be related to their complicated functions.

In this regard, it is noteworthy that some juveniles had deformities primarily of the hindlimbs and less of the forelimbs (Fig. 13). The legs progressively calcify during the period of nesting in altricials, containing about one percent calcium at hatching but an average of six percent at fledging (O´ Connor 1984). It is possible that in the granite conditions of the high mountain environment, juveniles suffer calcium deficiency in their legs during the extremely rapid development of all limbs. Additionally, some chicks have been found with broken legs immediately after leaving the nest. Previous research on passerine species has established that young reared on diets low in protein had shorter tarsi and lower mass because of lower growth during the nestling period (Boag 1987).

Fig. 13. Young immediately after leaving the nest. The juvenile has a visible deformity of the right leg with atypically developed claws. On the left healthy leg there are visible pads for movement on rocks. The outer toe has a 1-1-1-1 pad distribution, while the other toes have pads reinforced on the middle toe links. The pads protect the foot from sharp surfaces even in the cold and frost. The outer toe also needs to be more flexible for other activities, such as cleaning. 2006, Tatra mountains. (Photo: M. Janiga).

Hatching asynchrony

There has been considerable interest in the reproductive strategies of alpine accentors, in particular the maximization of reproductive output by parental birds through control of the mortality pattern and growth of their young (Nakamura 1990; Davies *et al.* 1995, 1996). Probability of survival of young may not be constant within broods, depending on: the exact allocation of reproductive effort by parents to individual eggs and nestlings; the state of incubation in relation to egg laying; and environmental conditions such as the number of adult individuals feeding the young, and the size and predictability of the food supply (Hartley *et al.* 1995; Heer 1996). Alpine conditions may be the cause of this in alpine accentors, as partially reduced asynchronous hatching has been observed. The female usually searches the nest during the egg-laying period only for oviposition and does not spend the night in the nest. In clutches with three or less eggs, the female starts incubation after laying the last egg. When laying four eggs, she usually goes to the nest in the evening of the third day and starts to breed regularly the following day (Heer 1998). This means that alpine accentors cannot afford the high diversity index in eggs in extreme climatic conditions of some other songbirds. In the species *Corvus frugilegus* (raven), for example, the index of growth speed of embryo is 3.2, which means the embryo develops to 18th stage of embryogenesis in five days after hatching. If the embryo had the rate of development of the last egg laid, it would have reached the 24th stage of embryogenesis (Bolotnikov *et al.* 1985). In alpine accentors, the first two to three eggs (Glutz von Blotzheim and Bauer 1988) and the fourth to sixth (Cramp 1988) eggs may differ in length of incubation by more than 24 hours, though this interval may be somewhat shortened at hatching (Table 1). In a three-egg clutch, Dyrcz (1976) observed hatching between 10 p.m. at night, and 8 a.m. the following day, with all the chicks hatching at the same time. The last hatchlings to hatch are less likely to spend a shorter time in eggshells, related to the energetic capabilities of the individual eggs. The embryos of the first-laid eggs produce thermal energy at the expense of fat, which they usually have more of than the last-laid eggs, increasing the energetic role of proteins and carbohydrates in the latter (Belikov 1975; Kamenskii *et al.* 1975).

Allometry

Much of the variation in growth of altricial birds can be attributed to differences in body mass. In general, the growth-rate of altricial species with similar mass can significantly vary in interspecific as well as intraspecific level (Johnston and Janiga 1995; Starck and Ricklefs 1998). Differences in the growth-rate among individual birds in a nest can manifest as morphological differences of differential timing in the growth and maturation of certain body components and organs (Janiga 1992a, b, c). Young may be growing at the maximum rate allowed by cell function and physiology resulting in an addition of body mass in overfed young. This means, for example, that an ontogenetically well-defined superiority in the development and growth of feathers causes a temporary reduction in the growth-rate of other organs, often expressed numerically in terms of mass (Novotný 1958). In altricial nestlings from better environmental conditions, body weight has a higher growth-rate relative to wing length, and wing length has a higher growth-rate compared to the growth-rate of body weight in young reared in poorer conditions (Beľskii 1948; Novotný 1970, O´ Connor 1984). Experimental feeding of altricial bird species intensifies weight growth stages and delays the onset of feather differentiation (Belskii 1948; Johnston and Janiga 1995; Konarzewski *et al.* 1996). Adaptation to harsh alpine conditions in alpine accentors is illustrated in the form of allometry of growth primaries and body weight in Figure 14. Hatchlings develop at about the same growth-rate during the first half of the nestling period. Younger nestlings have about the same growth-rate as their older siblings, only lagging behind them in development based on the time of hatching. Hence, the feeding family of adults does not prefer some of the nestlings, feeding them all equally. In the second half of the nestling time, the rate of feather growth relative to weight is higher in the younger chicks than in their older siblings. In older nestlings, feather growth slows down as the weight of the internal organs increases, which means that by the time the nestlings leave the nest, the younger and older siblings are already at approximately the same developmental level. This is accomplished within a period of two or three days, when the young begin to move among the rocks.

From the moment the young birds leave the nest, they begin a life of independence, or at least less dependence, as they gradually acquire efficient flight skills during the post-fledging period. Compared to adults, juveniles have inferior flight performance, including lower speed, lower wingbeat frequency and amplitude, and shorter daily flight distance (Heers *et al.* 2016; Rotics *et al.* 2016). The general trends observed in birds suggest that feather microstructure is likely to have a more dramatic effect on wing aerodynamics than gross wing morphology (Dial *et al.* 2006; Heers *et al.* 2011). The development of the alpine accentor is characterised by a linear increase in wing length and body weight during the post-fledging stage (Fig. 15). This means that in the juvenile stage, when birds are already actively flying, they are still growing, increasing not only the surface area of the feathers but also the weight, represented by the thickening of the wing and pectoral musculature.

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Hatching asynchrony pattern	Number of cases	Hatching asynchrony pattern	Number of cases	Hatching asynchrony pattern	Number of cases
2 + 0	1	3 + 0	2	3 + 1	3
		2 + 1	7	1 + 2 + 1	1
		1 + 2	3	1 + 3	1
				2 + 2	2

Table 1. Pattern of hatching asynchrony in 20 alpine accentor nests in the West Carpathians. The eggs usually did not hatch all at once, the first group of nestlings usually hatched earlier (for example, three chicks in the pattern 3 + 1) , followed by the second group of eggs, which hatched from 0.5 to 1 day after the first chicks hatched (for example when one chick hatched later, the scheme of hatching asynchrony pattern was 3 + 1).

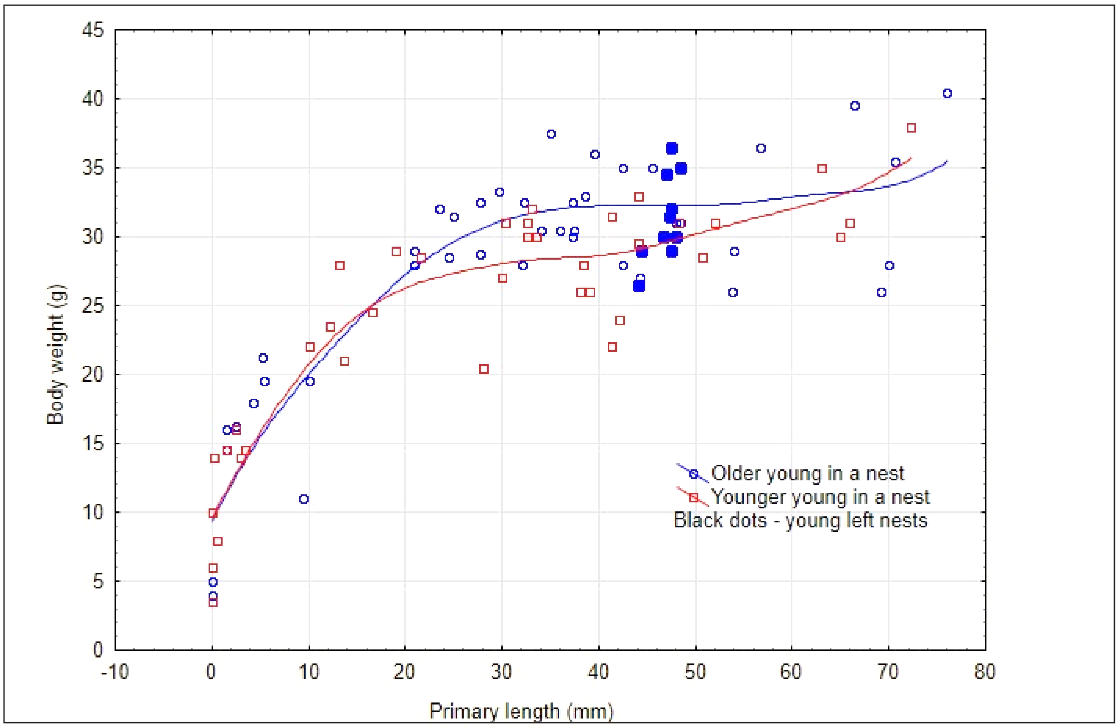

Fig. 14. Hatchlings grow at about the same rate during the first half of the nestling period, and younger nestlings grow at about the same rate as their older siblings, only lagging in development by the time they hatch. During the second half of the nestling period, the rate of feather growth relative to weight is higher in younger than older chicks. In the older chicks, feather growth slows as the weight of the internal organs increases, so that by the time the nestlings leave the nest, the younger and older siblings are already at the same developmental level. This is achieved over a period of two or three days as the chicks move around under rocks.

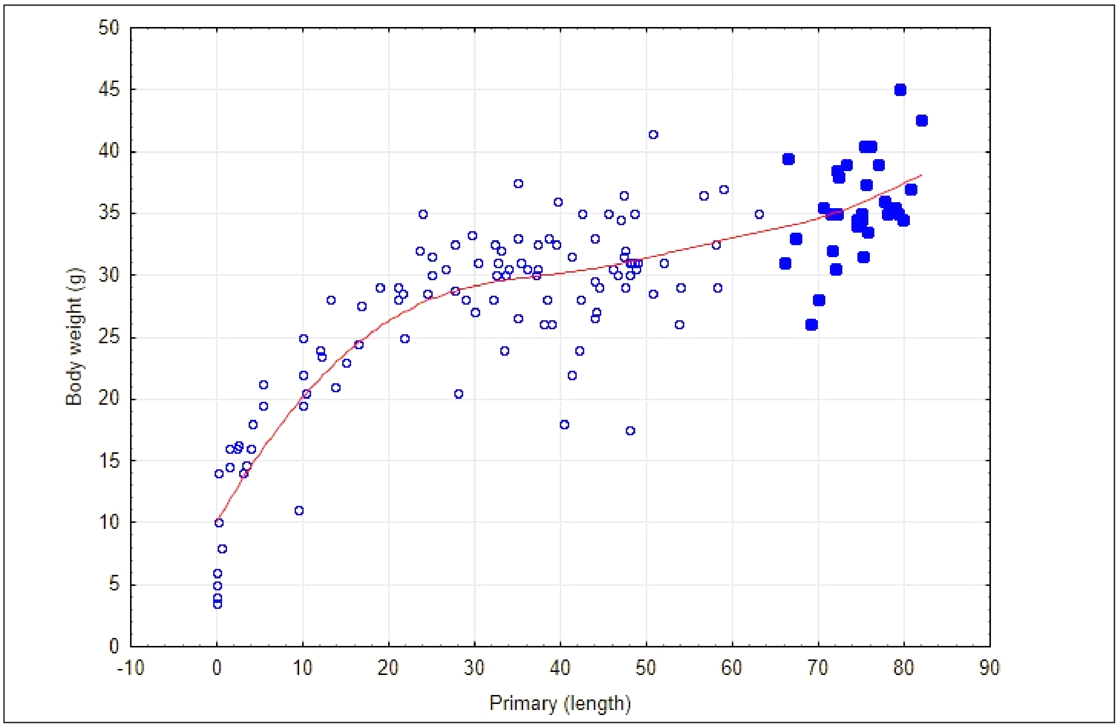

Fig. 15. Allometric relationship between growth of body mass and wing length. Juveniles older than 18-19 days of age and capable of active flight are marked with solid squares.

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