Bearded Reedling *(Panurus biarmicus)*: the biology of a remarkable bird – a review of the recent literature

Ádám Z. Lendvai

Abstract The Bearded Reedling *Panurus biarmicus* is a frequent, yet relatively little-known passerine bird found in wetlands across Eurasia. The species is difficult to study because of its elusive nature and the challenging access to its habitat: old, particularly dense reed patches standing in water. However, a detailed body of knowledge of the species' natural history, morphology, and behaviour has been gathered over the years, providing insight into the adaptations this unusual bird uses to survive and even thrive under favourable conditions. In 2023, BirdLife Hungary named the Bearded Reedling as the 'bird of the year'. In light of this notable designation, this article provides an overview of research advances on some of the unique characteristics of the Bearded Reedling, focusing on the factors that affect their population dynamics and potential conservation management strategies to protect the species.

Keywords: Bearded Reedling, *Panurus biarmicus*, reed, population dynamics, conservation

Összefoglalás A barkóscinege *Panurus biarmicus* egy gyakori, de viszonylag kevéssé ismert énekesmadár, amely Eurázsia vizes élőhelyein fordul elő. A faj nehezen tanulmányozható, mert fészkelőhelyét – a vízben álló öreg, különösen sűrű nádasokat – nem könnyű megközelíteni és ezért a faj megfigyelése kihívások elé állítja a kutatókat. Az évek során azonban részletes ismeretek gyűltek össze a faj természetrajzáról, morfológiájáról és viselkedéséről, amelyek betekintést nyújtanak abba, hogy ez a szokatlan madár milyen adaptációk révén képes fennmaradni, sőt, kedvező körülmények között látványos mértékben gyarapodni is. 2023-ban a Magyar Madártani és Természetvédelmi Egyesület a barkóscinegét választotta az év madarának. Ennek a választásnak az apropóján, ez a cikk áttekinti a barkóscinegéről és annak egyedi jellegzetességeiről szerzett legújabb kutatási eredményeket, a populációdinamikát befolyásoló tényezőkre és a faj védelmét szolgáló lehetséges természetvédelmi kezelési stratégiákra összpontosítva.

Kulcsszavak: barkóscinege, *Panurus biarmicus*, nádas, populációdinamika, konzerváció

Department of Evolutionary Zoology and Human Biology, University of Debrecen 4032 Debrecen, Egyetem tér 1. corresponding author, e-mail: az.lendvai@gmail.com

Introduction

The Bearded Reedling *(Panurus biarmicus)* is a small (~15 g), conspicuous passerine bird living in wetlands across Eurasia. It is an elusive bird species tied to wetlands all year round, and because its habitat is difficult to access, details of its biology have remained challenging to uncover. However, some enthusiasts of the species have gathered a surprisingly detailed body of knowledge of the species' natural history, morphology and behaviour. This

information has been excellently summarised and synthesised in a German monograph by Wawrzyniak and Sohns (1986). Since its publication, many other research has been conducted on the species, and we gained new insights into the species' distribution, social behaviour, reproduction, genetics and physiology.

In 2023, BirdLife Hungary (Hungarian Ornithological and Nature Conservation Society) selected the Bearded Reedling as the 'bird of the year'. In this context, I shortly review the recent research advances on the species, focusing on the factors affecting its population dynamics and discussing potential conservation management strategies to protect the species. Putting this information together may give us a better understanding of this charming and fascinating passerine species.

General description and taxonomy

The Bearded Reedling is a unique songbird in many ways. It is not closely related to any other passerine and belongs to its own monotypic family. It is a conspicuously dimorphic species, where sexual size and colour dimorphism may already be found at the nestlings stage, which persists and becomes even more pronounced later in juveniles and adults. It forms unusually strong pair bonds shortly after fledging and remains socially attached to its partner during its life while being sexually quite promiscuous. Reedlings do not hold and defend territories but usually breed semi-colonially in loose groups, where the parents cooperate closely to rear their young, sometimes by taking care of incubation and chick rearing in different broods simultaneously. They are confined to reed stands throughout their lives and possess a number of adaptations to be highly efficient in exploiting these habitats. They are not migratory but can travel long distances (often with their social partner or in small groups) to discover and quickly colonise new areas. They are insectivorous during the summer, but to adapt to seasonal changes in conditions, they change their gut morphology and switch to a chiefly granivorous diet during the winter using a food searching behaviour that is not found in any other Eurasian bird. Unlike almost any other bird in the Northern hemisphere, they may reach sexual maturity a few weeks following their independence and might initiate a second generation within the same year. In the following sections, I review our knowledge of these aspects.

Its name (somewhat counter-intuitively) originates from the NE European area around the White Sea, called Biarmia, where the species was never known to exist. The syllable 'bi' in the name misled many to believe that it refers to the Latin 'double' ('bis') and thus means 'with two beards' or 'with two daggers' referring to the birds' two pointy, triangular feather marks, as the 'armicus' may be confused with the Latin 'armatus' meaning 'equipped with weapons'. This interpretation led the Dutch zoologist C. J. Temminck to name the Lanner Falcon *Falco biarmicus*, because it also possesses a similar, characteristic dark facial pattern that he thought had given the scientific name to Bearded Reedlings (Jobling 2010).

The taxonomic classification of Bearded Reedlings has undergone several changes in recent years, with different authorities proposing different taxonomic arrangements. As its former vernacular name (Bearded Tit – which is still often used) suggests, it was believed to

be a relative of tits (Paridae), but its distinctive eggs, morphology, life history and behaviour soon revealed that it is not part of the true tit family (Bibby 1983). It has been variably classified among flycatchers (Muscicapidae), sylviid warblers (Sylviidae), parrotbills (Paradoxornithidae) and old-world babblers (Timaliidae). However, recent molecular studies showed that the Bearded Reedling is not closely related to any of those groups and is part of a distinct lineage that is a sister group of Alaudidae (larks) (Alström *et al.* 2006, Yeung *et al.* 2011, Alström *et al.* 2013). As a result, the species was finally moved to its own family, the monotypic Panuridae, as suggested before the advent of molecular phylogenies (Voous 1962, Bibby 1983).

Currently, three subspecies are recognised (Robson 2020). The nominate race, *P. b. biarmicus* occurs in Great Britain, France, Spain, Scandinavia, Russia, the Balkans, and Turkey. The other subspecies, *P. b. russicus* occurs in the Baltics, Poland and Belarus to Austria, NE Croatia, N Serbia and Montenegro, Bulgaria and Romania, Kazakhstan, Mongolia and China (Xinjiang, N Qinghai, W and NE Inner Mongolia, Ningxia, NE Heilongjiang). A third subspecies, *P. b. kosswigi* is used to be found in S Turkey and is now considered extinct (Saygili *et al.* 2013, Robson 2020). While the nominate race is somewhat darker, the morphological differences between these subspecies are subtle (Sluys 1983). However, even a single population may harbour morphological differences. For instance, wing length and morphology have been found to differ between sexes and age classes (Peiró *et al.* 2006). Adults have longer wings than juveniles, and females also have more convex (more round) wings than males after moult. These variations in wing morphology within the species suggest that different age groups and sexes may have somewhat different site usage. Females and juveniles with more convex wings may have enhanced manoeuvrability, while their ability to fly longer distances efficiently could be limited (Nielsen 1993, Peiró *et al.* 2006). A study of two Turkish populations showed morphological differences between the sites, but genetic analyses revealed sufficient gene flow between them (Saygili *et al.* 2013).

Habitat selection

As its new vernacular name suggests, the Bearded Reedling is a true reed specialist, and it is associated with reed *(Phragmites australis)* throughout all of its life stages and uses this habitat for foraging, nesting, roosting, etc. While the species may be found in other wetland vegetation types and sometimes may even prefer patches with mixed vegetation (Wawrzyniak & Sohns 1986), it remains mostly attached to extended reed beds. Sometimes it is stated that the species is mostly associated with cattail (*Typha* sp.) for breeding (Haraszthy 2019), but previous studies clearly indicate a preference for reed (Wawrzyniak & Sohns 1986). However, this may depend on the availability of different vegetation and may also vary between populations. For instance, in a Polish population, most nests were found in sedges (*Carex* sp.) (Stępniewski 2012), while in the Hortobágy Fishponds (Hungary), all nests were found in reed (n = 205), despite our efforts to locate nesting sites in pure or mixed cattail patches as well (Lendvai *et al.* unpublished results). Large-scale habitat analysis using remote sensing methods measuring vegetation structure directly over broad

extents and at a high resolution also revealed that the most reliable predictor of the species' presence in an area is the availability of reed, especially water reed, much more than land reed (Campbell 2021).

Habitat selection may change seasonally among different life-history stages, such as breeding, wintering or dispersing, and even within a single stage depending on the activity (nesting vs. foraging) or between individuals of different body conditions (Hoi & Hoi 2001, Trnka & Prokop 2006, Saygili *et al.* 2013, Peiró 2017). During the breeding season, reedlings prefer to forage in recently grazed or cut stands of reed, where there is higher availability of food and better foraging conditions due to lower vegetation cover. However, they breed mainly in highly structured reed, and they may undertake frequent and relatively long foraging trips from their nesting sites to the relatively open areas (Beemster *et al.* 2010). During the winter, when they switch to a predominantly seed-based diet, they prefer areas with a large build-up of reed litter (Bibby 1981, Wilson & Peach 2006, Beemster *et al.* 2010) that they search through for fallen seeds and occasionally invertebrates. When they do so, they often perform a typical searching movement: they hop forward and then suddenly pull the litter backwards simultaneously with both of their legs; a behaviour referred to as 'bilateral scratching' which only occurs in taxonomically completely unrelated groups (in the Americas and tropical Africa) (Greenlaw 1977).

Although the availability of nesting sites in (often vast) reed beds may seem infinite, this picture is considerably nuanced by the structure of the reed bed. For nesting, reedlings show a marked preference for dense, clumpy, fragmented reed, often forming tussocky 'reed islands' surrounded by water or, conversely, inner clearances in otherwise big patches of reed (Wawrzyniak & Sohns 1986, Hoi & Hoi 2001, Dadam *et al.* 2014). In accordance with this preference, in three different Hungarian wetlands, reedlings were found more often in dense reed, especially at the edge of open water (Báldi & Kisbenedek 1999). More recent studies also confirmed this pattern in NW Europe, where occupied nests were more likely found in old, uncut and dense reed patches (Malzer & Hansell 2017). Even among those areas, the birds preferred patches where the degree of reed compaction or stagger reached medium to high levels (Malzer & Hansell 2017). An experiment investigating nest predation on artificial nests also underlined the importance of reed compaction in reducing nest predation, especially for predators using visual cues and also by decreasing exposure to direct sunlight (Malzer & Helm 2015). Therefore, even in large areas where the reed forms homogenous sparse coverage, the reedlings may not find suitable microhabitats for nesting. Wawrzyniak and Sohns (1986) report a few cases where reedlings occupied nests of other species, indicating a potential limitation of suitable nesting places. Improving nesting prospects by providing artificial nest sites may be especially beneficial in these places (see section 'Conservation' below).

The availability of suitable breeding, sheltering and foraging sites may vary not only within a particular wetland, but also at the landscape level. While there are enormous reed stands in some wetlands, on a large geographical scale, this habitat is essentially and inevitably fragmented as it is connected to the patchily distributed water bodies. Furthermore, on a longer temporal scale, reed stands may represent a transitional stage of succession, as with eutrophication and accumulation of leaf litter, it tends to transform into scrublands unless the leaf litter is periodically removed e.g. by regular flooding. Therefore it is expected that

a bird that is confined to this sole habitat may have evolved strategies and behaviours to move between these patches depending on the current conditions. This is discussed in the next section.

Movements

The Bearded Reedling is a resident species throughout most of its range, and the species is not known for exhibiting typical migratory behaviour (but see Dürr *et al.* 1999 for a possible exception). However, a characteristic part of their life cycle is the eruptive dispersion (Spitzer 1972, Pearson 1975, Wawrzyniak & Sohns 1986, Cramp & Perrins 1994, Fenyvesi 1999a). This behaviour usually builds up as an accumulation of increasing restlessness and excitement of the birds. Some birds climb up in the reed stems and fly above the reeds with loud vocalisations, then initiate a vertical flight up to 20–30 meters while other members of the group join them, continuing loud calls. Following erratic movements, the flock eventually drops swiftly back to a different part of the reed stand. This process is repeated across several days, usually with peak intensity in the morning hours. After some days, some of these 'high-flying' does not end in plunging back to the reeds but may culminate in wandering long-distance dispersal.

   Analyses of recapture data based on focal countries have concluded that this dispersal is different from migration in the sense that the eruptive flights lack a clear directional bias but instead show scattered, star-like movements out from a central location (Cramp & Perrins 1994, Hořák *et al.* 2003, Peiró 2013). Ring recovery analyses from Hungary has also confirmed this pattern (Mogyorósi 2009, Bukor 2023). Clearly, these movements are different from the traditional passerine migration pattern. For instance, unlike in many passerine species, the dispersal behaviour of the reedling does not show clear sex or age effects (Malzer 2017), although juveniles may reach the peak of these movements somewhat earlier (Gyurácz *et al.* 1997). However, a more recent analysis based on over four thousand recaptures on a Pan-European scale revealed that there is some regularity in the seasonal and directional pattern of the reedling movements. During the fall, Northern, Western and Eastern populations are more likely to move towards the South than in other directions, and the reverse direction can be observed during spring (Malzer 2017, Spina *et al.* 2022). These results suggest that despite the irregularity of their movements, there are some overall trends, and the species may be classified as a partial migrant (Malzer 2017).

Distribution and population dynamics

There have been several studies on the temporal dynamics of local Bearded Reedling populations, which have shed light on the factors that influence their distribution and abundance over time. These studies have shown that Bearded Reedlings are relatively resilient to short-term environmental fluctuations, but they can be affected by long-term changes in habitat quality and fragmentation.

One important factor that can influence the temporal dynamics of Bearded Reedling populations is weather conditions, particularly during the winter months. Harsh winters with prolonged periods of snow and ice cover can lead to reduced foraging opportunities, which can result in dramatically reduced survival and breeding success (Bibby 1983, Wawrzyniak & Sohns 1986, Cramp & Perrins 1994, Wilson & Peach 2006), but see (Surmacki & Stępniewski 2007). These adverse conditions can sometimes lead to local extinctions (extirpation), particularly in areas where Bearded Reedlings occur at the edge of their range (Wawrzyniak & Sohns 1986). For instance, in Hungary, it has been recorded that after the freezing winter of 1939, during the breeding season of 1940, only a few birds could be observed in an otherwise large breeding population. Following a temporary recovery, another harsh winter in 1941 wiped the birds from at least two large populations in Hungary with extensive reed beds (Dinnyés and Kis-Balaton) (Vönöczky Schenk 1942). Similarly, in Belgium, the species disappeared in the 1920s, reappeared only in the 1940s and became frequent twenty years later (Tahon *et al.* 1968).

Conversely, following the collapse of some of the local populations, another characteristic of the species is the ability to recolonise areas and spread quickly. A striking example of this recovery is the dynamics of the species in NW Europe, which underwent extreme fluctuations in the middle of the 20th century. For instance, the breeding population in Britain had declined significantly by the end of the 19th century due to the combined effects of habitat destruction, egg collection and the trade of adults as cage birds. This was exacerbated by several harsh winters in the 1930s and 1940s that were characterised by unusually cold weather and significant precipitation. In particular, following the winter of 1946–47, which saw prolonged heavy snowfall and icy conditions, the available food sources became so limited that the population virtually disappeared (O'Sullivan 1976). However, from the 1950s onwards, the population recovered and even became a source for rapid expansion in W Europe (Wawrzyniak & Sohns 1986).

A spectacular example of the latter phenomenon was the repopulation and the exodus following the collapse of the British population. This process has been well documented (O'Sullivan 1976, Wawrzyniak & Sohns 1986). A stable population of the species is thought to have existed in the Netherlands, but its numbers have followed the changes in the size of the extensive reed beds to a considerable extent. From 1959, the draining of polders initially resulted in the formation of vast reedlands, which was followed by the reclamation of these lands and the concomitant decrease of the reed-covered area. The rate of retreat of the reed beds was so great that over the course of a decade their initial extent was reduced by more than an order of magnitude, and it is assumed that this sudden decrease of suitable habitat contributed to the dispersion of the birds (Wawrzyniak & Sohns 1986). The initially vast reed beds are thought to have harboured a large (exceeding 10,000 pairs) population that may have served as a reserve from successive colonisation waves (Houwen 1967). During this period, reedlings appeared where they had previously been absent. Around 1965, they appeared and established new populations in Belgium and shortly afterwards in Northern and Western (even Atlantic) France, inland Germany and Poland. By the end of the 1960s, they had also appeared on the Scandinavian Peninsula, where the species had previously been entirely absent. From 1965 until the early 1970s, the colonisation of Denmark and

Sweden continued, and by 1977, the number of overwintering birds was estimated to be over 20,000 individuals (Wawrzyniak & Sohns 1986). These newly formed populations also exhibited wild year-to-year fluctuations as documented for the species in other areas, as exemplified by one Swedish population that, over four years, dropped back from an estimated 5,000 to 100 breeding pairs (Wawrzyniak & Sohns 1986).

The fluid dynamics of the populations, the disappearance of some and the colonisation of new breeding areas were not restricted to a particular period in the 20th century. This ongoing process has been recently documented in the local ornithological literature for the Southern and Eastern front of the European expansion (e.g. Fedorov 2015, Ječmenica 2016, Berezovikov & Rozenberg 2019, Koshelev & Cherkasov 2019). These sudden influxes of Bearded Reedlings may be related to weather patterns, food availability, and habitat suitability. For instance, the appearance of massive reed beds in new areas may facilitate the distribution of the species in new places (Berezovikov & Rozenberg 2019). As a consequence, trends of the European populations show a very diverse picture, with the Hungarian population trend being stable but also uncertain (Nagy 2021).

Overall, the temporal dynamics of local Bearded Reedling populations are influenced by various factors, including weather conditions, habitat quality, and fragmentation. While Bearded Reedlings are relatively resilient to short-term environmental fluctuations, they can be affected by long-term changes in their habitat. Understanding these dynamics is crucial for effective conservation management, particularly in areas where Bearded Reedlings are considered to be threatened or endangered.

Mate choice, pair-bonding and reproduction

One fascinating aspect of the Bearded Reedlings' biology is their capacity for fast reproduction, which may explain the rapid (re-)colonisation of new areas and then the rapid expansion. This may be enabled by a combination of traits that would put them on the extreme fast side of the slow-fast life history continuum (Dammhahn *et al.* 2018).

A fast life history pace starts with an early pairing. Soon after hatching, juvenile Bearded Reedlings form small groups and move around the habitat together. During this period, attachments form quickly between males and females (although typically this does not occur between siblings, but see Marin *et al.* 1994), and these alliances may develop into early pair-bonds. This phenomenon was already described by Koenig (1951), but how long these young pairs stay together and how durable their relationships have remained an open question (Wawrzyniak & Sohns 1986, Cramp & Perrins 1994).

It was also observed in the mid-20th century that these pairs move together, sometimes at large distances, e.g. birds ringed together in the Netherlands fell into a net together in NE Wales (Bibby 1983). The close association of the pair members allowed the investigation of this phenomenon based on capture-recapture data. One study found that individuals (putative pairs) captured close to each other simultaneously were often recaptured together, sometimes on several consecutive occasions, and statistical analyses showed a significant association between these individuals (Bártol & Csörgő 2000). Another study attempted to

identify captive pairs by including behavioural observations prior to the birds being caught in nets, and similarly to the previous study, also showed significant association between existing pairs (Lovász *et al.* 2017). However, the latter study was also able to show that a significant proportion of pairs formed at a young age remained together for longer periods, confirming previous hypotheses that reedlings form persistent, socially monogamous relationships. Based on the sex distribution of the captured animals, statistical probability calculations can also be used to infer the pair-bonds from mark-recapture datasets. Using this method, pair-bonds in a significant proportion of juveniles could be identified in two European populations (Brocchieri *et al.* 1992).

The early establishment of stable pair-bonds may be an important element in the successful reproduction of reedlings. Long-term pair-bonding can increase reproductive success and fitness in many species (Sánchez-Macouzet *et al.* 2014). In socially monogamous species, individuals that maintain pair-bonds over multiple breeding attempts are often able to improve reproductive success compared to conspecifics that switch partners (Gabriel & Black 2012). These benefits can manifest in Bearded Reedlings. The formation of stable pairs in the previous year facilitates an early onset of reproduction because they do not have to "waste time" on choosing a mate in spring (Bibby 1983). Egg-laying typically starts around in early April in many European populations (Wawrzyniak & Sohns 1986). However, it should be noted that some pairs may start breeding significantly earlier. For instance, in 2016, in the Hortobágy Fishponds, Hungary, we observed a fledgling on the 4th of April, which, even based on the most conservative estimate, suggests a clutch initiation in early March (Lendvai *et al.* unpublished data). This may precede by at least two weeks the earliest onset of laying found in the published literature (Stępniewski 2012).

Such an advancement of breeding, even in a species that starts reproduction early in the season, may be the consequence of the well-coordinated cooperation of pair members. It was experimentally demonstrated that longer periods of forming pair-bonds lead to better overall breeding performance than those with shorter periods, resulting in more synchronised nest building, the higher success rate in nesting, and earlier clutch initiation (Griggio & Hoi 2011). Importantly, these differences were not due to different efforts of the parents, highlighting the importance of pair coordination. The effect sizes of these factors are far from subtle: birds in well-established pair-bonds may start up to one month earlier and can have twice as many offspring in a season than hastily paired individuals, conferring a strong evolutionary advantage of strong social monogamy (Griggio & Hoi 2011).

If pair-bonds are that important, we may expect that birds are ready to strengthen it during hard times. This is exactly what happens, as an elegant experiment demonstrated (Hoi & Griggio 2012). When monogamous pairs were isolated and presented with an unpaired solitary conspecific, the pair members increased physical contacts with each other to reinforce their pair-bond. However, this response depended on the sex of the unpaired bird. Females initiated more contacts with their mates only if the single individual was a female and thus, a potential competitor. In contrast, male partners increased the number of contacts with their mates if the competitor was a male, but also if the lone individual was a female that was less attractive than their mate. These results suggest that reedlings adjust their pair-bond investments in response to the presence, and to a lesser extent to the

attractiveness of a potential rival (Hoi & Griggio 2012). Social cohesion between the pair members may be reinforced by vocalisations, clumping together, and mutual allopreening (Tóth *et al.* 2015).

Given the importance of the relationship, choosing a good-quality mate is crucial with respect to fitness. As reedlings do not hold territories, mate choice is based on individual quality and their decision is not determined by resources. Since pair formation already happens in juveniles, one might expect to find sexual dimorphism in juveniles. While this is rare in passerines, reedlings represent a conspicuous case for such a phenomenon (Surmacki *et al.* 2015).

Males and females have different bill colouration that is already noticeable at the nestling stage and can be used to reliably determine the sex of the chicks (Darolová *et al.* 2008). This difference in bill colouration remains after fledging and persists until adulthood. While juvenile males do not have 'beards' as adults do, they have black lores that also shows sexual dimorphism. Juvenile males have larger and more conspicuous, darker lores, a more extensive melanised back patch, while they also have significantly longer tails and are in general, larger and heavier than females (Surmacki *et al.* 2015). Back patch size in juvenile males was also related to their body condition, suggesting that these sexually dimorphic traits may serve as condition-dependent signals.

In adults, two important feather quality markers are the "beard" of the males and the length of the tail (in both sexes). Beard length is negatively related to parasite load and is the best predictor of dominance in male-male competition (Hoi & Griggio 2008). Nevertheless, it is a static signal that is not related to body condition (Hoi & Hoi 2001, Peiró 2021), and it only changes during the annual moult, whereas dominance behaviour is much more dynamic and reflects the actual state of the individual. When females had to choose between males of experimentally manipulated beard length and males with different social status (dominant vs. subordinate), they showed a clear preference for long-bearded males, with dominance status having only a slight complementary effect (Hoi & Griggio 2011).

Beard length may play an important role in males' life if their partner dies. Females have higher mortality than males (Peiró 2011), and if an older male loses his partner, it is frequently observed that he joins juvenile flocks and forms a partnership with a new mate (Hoi & Griggio 2008, Lovász *et al.* 2017). Having an attractive long beard in this context may be advantageous. However, instead of having the largest beard possible, having any beard in the first place may be even more important. Juveniles and adults all perform a complete moult at the end of the summer, and the sequence of the moult is strictly regulated (Steiner 1971, Buker *et al.* 1975, Pearson 1975, Massi & Spina 1996). The head feathers and the beards are among the last body parts moulted, so completing the moult sooner and get it ready when pair formation and mate choice happens may be more important than having a large beard but too late (Hoi & Griggio 2008). (For the physiological mechanisms that may allow faster development of the sexually selected ornaments, see the section 'Physiology' below). Beard length is also positively related to extra-pair copulations (see below) and negatively associated with parental contributions (both incubation and chick provisioning) (Hoi & Hoi-Leitner 1997). These results clearly indicate that sexual selection plays an essential role in the evolution of this ornament.

Another trait that is under sexual selection in Bearded Reedlings is the tail. Males have longer tails than females in both adults and juveniles (Cramp & Perrins 1994, Surmacki *et al.* 2015). Females prefer males with longer tails, and while males may also find short-tailed females less attractive, their preference for long traits may be less pronounced than in females (Romero-Pujante *et al.* 2002). Therefore, tail length seems to be a quality indicator in both sexes and is a subject of mutual mate choice. Females with longer tails have better body condition and larger clutch sizes (Hoi & Hoi-Leitner 1997).

Apart from sexual selection, tail length is also affected by natural selection, as the length of the tail affects movement agility. In an experiment where the tail was shortened, individuals used the characteristic straddle posture (when they use both legs to hold on to different reed stems) less frequently (Romero-Pujante *et al.* 2005). However, tail length (and also beard length) is not related to the birds' social position or prestige in the flock (Tóth *et al.* 2015).

Both adults and juveniles bear multiple ornaments, bringing the question of how individuals evaluate their information content during mate choice. This question was investigated in an experiment where manipulation of these two traits in males was conducted to convey conflicting messages about the quality of the bearer. When females were presented with contrasting information about beard length and tail length, a preference polymorphism emerged, with some females showing a strong preference for the tail while others for the beard (Griggio *et al.* 2016).

While long tail may be a quality indicator in both sexes, the fact that males do not show an unambiguous preference for long-tailed females (as described above) may be explained by the costs of having a high-quality female (Hoi & Hoi-Leitner 1997). High-quality females (with longer tails and better body condition index) breed in loose colonies, while some individuals are solitary breeders, building nests further away from the colony (Hoi & Hoi-Leitner 1997). The colonial females engage in a 'catch me if you can' game that puts their partners to a thorough test.

This characteristic behaviour is the chase-flight, a form of 'flirting-teasing' behaviour initiated by the females. The sequence of this behaviour usually starts with the female uttering a distinctive soliciting call that drives her partner and other males in the vicinity to attempt to copulate with her. However, before this could happen, the female suddenly escapes and flies up above the reeds while emitting calls, with her mate pursuing her. Other males join the chase (up to 12 males have been observed) (Birkhead & Hoi 1994). Eventually, the female turns suddenly and dives back into the reeds. Here the male that managed best to keep up with her has a chance to copulate, who is not necessarily the social mate. This phenomenon leads to a high degree of extra-pair paternity, although males with longer beards are better at protecting their paternity (Hoi & Hoi-Leitner 1997). Experimental tests have shown that females in their fertile period (nest-building and egg-laying) and high-quality females are more likely to initiate these chase-flights (Hoi 1997, Hoi & Hoi-Leitner 1997). Females therefore seem to incite male-male competition to assess the quality (in terms of virility and vigour) of males and thus, acquire extra-pair fertilisations to obtain 'good genes'.

This idea is further corroborated by the observation that males in this species have testes 70% larger than predicted by their body mass and they possess a phallus-like copulatory organ that is unique among passerines, while the females' reproductive tracts do not show

specific adaptations to avoid unwanted copulations (Birkhead & Hoi 1994, Sax & Hoi 1998). Furthermore, females have limited capacity to store sperm and have a relatively high rate of sperm loss that requires frequent copulations to ensure the successful insemination of the clutch during egg-laying (Sax *et al.* 1998). Taken together, colonial breeding may represent opportunities for the females to acquire extra-pair copulations. Colonial breeding is also associated with an increased incidence of conspecific brood parasitism in relation to nesting density (Hoi *et al.* 2010).

Once the pair is established, they soon start building the nest (with both sexes participating) and the female starts egg-laying. Eggs are white to creamy-white with fine dark brown line markings and speckles. Egg dimensions (based on 125 eggs from 19 nests collected in Hungary between 1926–1960): length 15.8–19.0 mm, breadth 13.1–15.1 mm, volume 1.42–2.15 cm³ (Solti 2010). Incubation usually starts with the penultimate egg, and both parents incubate. Nest building continues during incubation, especially lining up with feathers (Koenig 1951, Wawrzyniak & Sohns 1986). Clutch size is usually between 4 and 8 eggs (in Hortobágy, average 5.58 ± 0.88 SD, Lendvai *et al.* unpublished data, which is in agreement with other populations, but lower than 6.77 ± 1.0 reported earlier from Hungary (Wawrzyniak & Sohns 1986, Haraszthy 2019). Large clutches (up to 12 eggs) may represent egg dumping, which occurs frequently in the species (Wawrzyniak & Sohns 1986, Hoi *et al.* 2010). Clutch size may show significant yearly variation, and the repeatability of egg measurements is moderate, suggesting considerable phenotypic plasticity (Surmacki *et al.* 2003).

The chicks hatch about 10–13 days after laying the last egg. The secondary sex ratio of offspring (around the age of 7 days) from three populations was slightly, but not significantly female-biased. In a Spanish population, the juvenile sex ratio was also close to equity (Peiró 2011). However, in a study across three populations in Central Europe (Austria, Slovakia and N Italy), almost a third of the nests contained single-sexed broods, which deviated significantly from the expected under a binomial distribution (Darolová *et al.* 2009). Female nestlings tend to hatch sooner and have higher initial body mass than males, which, in turn, develop faster. By modifying the hatching order, female parents may give their daughters a head start in intra-brood competition (Darolová *et al.* 2008). Both parents feed the chicks, which fledge around 12–14 days, although chicks may leave the nest (force-fledging) earlier (after 9 days of age) if disturbed (Wawrzyniak & Sohns 1986, Haraszthy 2019).

There are some reports on cooperative breeding (Koenig 1951), but this has not been confirmed. Different adults or juveniles may often visit a nest of a focal pair, but whether they actively feed the young has not been demonstrated convincingly. In the Hortobágy Fishponds, in one nest with nestlings, we also trapped an adult individual that was known not to be either of the parents (which were both marked at this point), but we could not prove that this third adult was provisioning. In video recordings of several nests with marked parents, we never observed foreign individuals assisting in nestling provisioning (Lendvai *et al.* unpublished results).

Reedlings are multi-brooded. The number of subsequent broods may vary, usually 2–3, but it may be up to four broods in a season if environmental conditions are favourable (Buker *et al.* 1975, Wawrzyniak & Sohns 1986). Although the breeding season of the reedlings is

long – birds may still breed in August (e.g. Surmacki & Stępniewski 2007), to pull this off, the parents may need to resort to unusual solutions.

The stable pair-bond described above allows for very efficient cooperation between the parents, and this, in turn, enables the division of labour between the parents and initiating overlapping broods. When the nestlings are close to fledging, the couple may start building a new nest, sometimes giving "the impression of having been put together in undue haste" (Bibby 1983) and start egg-laying. A systematic study in Poland found that overlapping nesting attempts by the same couple are relatively frequent and consist of a median of 10% of the broods (Stępniewski & Halupka 2018). However, this feat was only observed when the population density was low. In years with high population densities, overlapping broods were never observed (Stępniewski & Halupka 2018). By initiating broods simultaneously, finishing nest building during incubation, sometimes reusing the same nest for subsequent breeding (Stępniewski 2003) and rearing their young to independence quickly, reedlings may compress all breeding stages and maximise the number of breeding attempts in a season.

In addition to these already remarkable attributes, reedlings possess another trait that further distinguishes them from other species, which is an impressive feature of their reproductive biology. As discussed above, juveniles pair up shortly after fledging, and it has been suggested that these juvenile pairs may start reproducing later in the season when they are born. This was indicated in two earlier observations (Spitzer 1972, Björkman 1975), and in captivity, juvenile pairs have been confirmed to build nests and lay eggs (Griggio & Hoi 2011), but it remains uncertain if these pairs can successfully finish a breeding attempt. Despite intensive field efforts, no such case has been unambiguously reported from the field in the past 50 years, so the phenomenon may be genuinely rare. Similar to overlapping broods discussed above, it is possible that this strategy occurs only in special years, with low breeding density, or during the initial phase of population establishment. Regardless of its frequency, the mere existence of this pattern, even if it exists only as a preparational step for the young couples for the following breeding season is remarkable, as no bird in the Northern Hemisphere has two generations in one year, with the possible exception of the Zitting Cisticola *(Cisticola juncidis)* (Ueda 1985).

Taken together, a suite of reproductive traits put the Bearded Reedling on the fast extreme of the slow-fast life history continuum. These include an early pair formation, strong life-long pair-bonds that allow the early onset of breeding, optimising parental cooperation and division of labour facilitating multiple, sometimes overlapping breeding attempts and eventually a juvenile reproduction, and thus, potentially a second generation within a season. All of these may contribute to the long-term resilience of the species in the face of environmental variation and the ability to increase population size, which is counterbalanced by their sensitivity to environmental conditions and high mortality rates.

Parasite infections

Apart from the climatic challenges, bearded reedlings, like most passerines also need to cope with the risk of parasitic infections, which can threaten their long-term survival. As

an obligate wetland-dwelling species, Bearded Reedlings live year-round in habitats that harbour a vast diversity of mosquitos that transmit various *Plasmodium* and *Haemoproteus* lineages. Various songbirds living in much drier habitats often have around 60% prevalence of malaria (Malavi database: http://mbio-serv2.mbioekol.lu.se/Malavi). In light of these data, it is surprising that we found an extremely low prevalence of avian malaria infection in two Central European populations 3.9% and 0% in Austria and Hungary, respectively: Szöllősi *et al.* (2020) and these results were corroborated by other populations: 3.8% in Bulgaria (Dimitrov *et al.* 2018), 10% in Sweden (Nilsson *et al.* 2016) and 0% *Plasmodium* while 3.4 and 10.3% in different *Haemoproteus* strains, respectively (Ciloglu *et al.* 2020). These results suggest two possible explanations. First, reedlings may be extremely sensitive to malaria infections with almost all infected individuals suffering high mortality (Szöllősi *et al.* 2020). While at the moment, we cannot rule out this possibility, given the large abundance and diversity of vector fauna in their habitat, if malaria eliminated all infected individuals, that would easily drive the population to extinction in a short time. The intriguing alternative explanation is that reedlings may be resistant to malaria infection or that birds are able to avoid or clear the infection quickly, which makes them an interesting potential model for the behaviour, physiology and genetics of immunity (Szöllősi *et al.* 2020).

Despite the remarkably low incidence of blood-borne parasites, Bearded Reedlings are hosts to a number of ectoparasites, including some host-specific species. The parasite causing the most conspicuous adverse effects in the birds is a newly described mite species *Harpirhynchus dusbabeki* (Bochkov & Literák 2006). This mite may have been previously misidentified as *H. nidulans,* and it induces the development of voluminous dermal cysts under the birds' wings (Henry *et al.* 2004, Bochkov & Literák 2005, Literák *et al.* 2006). The cysts take months to develop and therefore are only found in adults and show marked seasonal and geographical variation (Henry *et al.* 2004, Literák *et al.* 2005). While the mites do not cause immediate mortality and the fitness costs induced by them are not obvious, at least there is no observable effect on body mass and feather moult (Henry *et al.* 2004).

In addition to *Harpirhynchus dusbabeki / nidulans*, reedlings are hosts of feather mites *(Proctophyllodes pinnatus)* (Vágási & Tökölyi 2005), and may be infested with chigger mites *(Blankaartia acuscutellaris)*. In a population in southwest Slovakia, chigger mites were present on Bearded Reedlings throughout the year, but their prevalence and intensity of infestation were higher in the breeding season (Trnka *et al.* 2023). Although mite infestation in Bearded Reedlings has a relatively high prevalence and intensity, there seem to be no discernible differences in body condition between infested birds and those that are not. Therefore, it is suggested that infestation by *B. acuscutellaris* may not have serious negative effects on the health of the host, although the presence of ectoparasites could still have adverse effects, such as reducing the host's ability to cope with other stressors or infections. One study found 33 different mesostigmatic mite species in Bearded Reedlings nests collected from Austria, Slovakia and Italy, most of the mites belonging to the parasitic *Ornithonyssus sylviarum* species (Krištofík *et al.* 2007).

Another potential threat to reedlings is infection by the ticks, *Hyalomma rufipes*, which has been reported in recent years (Keve *et al.* 2023). This tick species is known

to carry various diseases, and its presence in reedling populations raises concerns for potential health impacts. Molecular analyses of the collected ticks showed that all *H. rufipes* individuals collected in Hungary had identical haplotypes, indicating a common maternal origin. Moreover, the study found that *H. rufipes* haplotypes were site- and population-specific, suggesting a potential founder effect in the population of *H. rufipes* in the southwestern part of Hungary. The apparent unengorged state of a *H. rufipes* larva on one of the birds suggests that the tick infestation did not originate from abroad but was acquired locally.

While none of these parasites seems to exert immediately harmful effects on the reedlings (with the potential exception of haemosporidian, see above), the effects of parasites on their hosts may be more subtle and indirect or dependent on their life-history stage, therefore, it is possible that in conjunction with other factors, they may contribute to variations in survival or fecundity.

Physiology

Recent years have seen an increase in the number of studies examining hormonal regulation in Bearded Reedlings, shedding light on the species' physiology and behaviour. One such critical hormonal aspect is the evolutionarily highly conserved insulin-like growth factor-1 (IGF-1) signaling pathway, a complex signaling network processing information about the internal state of the organism and regulating cell growth, differentiation, and survival. The IGF-1 system is extensively studied in laboratory model organisms but is much less known in free-living vertebrates, let alone birds (Lodjak & Verhulst 2020, Regan *et al.* 2020). A handful of studies in wild birds have investigated how IGF-1 affects growth in nestlings, while its role in adults has remained unknown. Therefore, the Bearded Reedling became one such system, where information is accumulating about the regulatory role of IGF-1 in avian systems.

In an initial experiment, we investigated the change in circulating levels of IGF-1 and corticosterone in response to stress in adult wild Bearded Reedlings. We found that during capture and handling stress, corticosterone levels increased, as seen in many other birds (Bókony *et al.* 2009). At the same time, IGF-1 levels significantly decreased, independently from glucocorticoids (Tóth *et al.* 2018). A follow-up experimental increase of corticosterone using a non-invasive oral manipulation revealed no effect on IGF-1 levels, suggesting that the hypothalamic-pituitary-somatotropic (HPS) axis producing IGF-1 may play an important role as a regulator of life-history decisions in response to unpredictable stressors (Tóth *et al.* 2018).

Another experiment investigated the role of IGF-1 during periods of food shortage by altering the feeding regimes in captive Bearded Reedlings. The birds lost mass under food restriction, but the magnitude of mass change depended on the initial dietary conditions, showing that individuals may anticipate future resource availability based on previous experiences and adjust their physiology accordingly (Tóth *et al.* 2022). We also found large individual differences in IGF-1 reaction norms, with some individuals increasing

IGF-1 levels in response to a restricted diet while others showed no response or decreased IGF-1 levels. These individual differences were explained by differences in average body mass, with heavier individuals having higher IGF-1 levels during the control treatment and being more likely to decrease IGF-1 levels in response to dietary restriction than lighter individuals. Males also had higher IGF-1 levels than females, but this may be due to their size differences rather than sexual differences per se (Tóth *et al.* 2022).

Finally, in a series of experiments, we investigated the role of IGF-1 in the formation of new feathers and the development of plumage ornaments. Using a novel experimental method (Mahr *et al.* 2023a), we achieved a sustained elevation of circulating IGF-1 levels using a single subcutaneous injection. In one experiment, we found that in naturally moulting juvenile reedlings, the IGF-1 treatment did not affect the feather growth rate of growing primary feathers but increased the number of feathers being moulted simultaneously and advanced the stage of moult. The birds with increased IGF-1 had better-quality feathers than the control group, as measured by the lower number of fault bars. An increase in IGF-1 may alter moult intensity by initiating the renewal of several feathers at once, shortening the overall moulting time, which may be critical in getting the plumage ready by the time of mate choice (see details above about the importance of early pairing for this species). However, this may imply costs in terms of IGF-1-induced oxidative stress (Lendvai *et al.* 2021).

This latter assumption was investigated in a different experiment, where we simulated elevated IGF-1 levels in captive Bearded Reedlings and found that increased IGF-1 causes short-term sex-specific oxidative damage. Males were more susceptible to IGF-1-induced oxidative stress than females and the capacity to quickly restore oxidative balance increased survival prospects in males. The study highlights a sexual difference in the physiological susceptibility to IGF-1 variation, which is intriguingly the opposite of earlier findings on laboratory mammals, where the mortality pattern is reversed compared to birds including Bearded Reedlings, where females generally incur higher mortality (Lendvai *et al.* 2023).

These results line up well with the observation that sexually selected ornaments seem to be related to IGF-1 levels in reedlings. A significant correlation was found between IGF-1 levels during moulting and the development of multiple ornamental plumage traits in male and female Bearded Reedlings. The results indicate that higher IGF-1 levels positively affected male structural plumage colours and tail feather length in males but not melanin-based ornaments, such as the beard length. Female tail length was also unrelated to IGF-1 levels. This is the first study that suggests that IGF-1 may play a role in the expression of sex-specific plumage ornaments in a bird species (Mahr *et al.* 2020). Because males seem more sensitive to IGF-1-induced oxidative costs, this mechanism may ensure the honesty of these sexual signals. These results are also corroborated by recent experiments, where the development of the structural colouration was affected by exogenously increased IGF-1 levels (Mahr *et al.* 2023b).

Taken together, IGF-1 in bearded reedlings may mediate life-history trade-offs between somatic growth (feather growth and the development of sexually selected plumage ornaments) and longevity (via IGF-1-induced oxidative stress in males).

Conservation

As noted earlier in this review, the Bearded Reedling show a combination of resilience and sensitivity to environmental effects. While in the long run, the species has managed to survive various environmental changes and achieved a widespread distribution, and thus, currently classified as 'least concern' by IUCN, local populations may be subject to dramatic declines and potential extirpation. Some of these cases in the recent past have been well documented. For instance, the population in Sicily went extinct by 1958 (Sluys 1983), just before the large range expansion in Western and Northern Europe detailed in the section 'Distribution and population dynamics'. More recently, the coastal populations in Spain suffered a dramatic decline, where the population collapsed and is predicted to become extinct shortly (Belenguer *et al.* 2016, Peiró 2022). The most well-documented fluctuation however, happened in the recently colonised high-latitude population in Leighton Moss, UK.

The first Bearded Reedlings arrived in Leighton Moss in 1965, during the great NW European expansion of the species (see 'Distribution and population dynamics'), and confirmed breeding from the early 1970s, then the population gradually stabilised to around 35 pairs in the 1990s (Wilson 1993). Later, the breeding population further increased to above 60 pairs by 2000 (Wilson & Peach 2006). Over the cold and rainy winter of 2000/2001, the leaf litter, which serves as a main reserve for seeds that the birds feed upon during the winter, got flooded, rendering the seeds unavailable (Bibby 1981, Wilson & Peach 2006). These events caused a general food shortage for the birds, resulting in suboptimal foraging options with increased exposure to predators, and the combination of these effects culminated in a massive drop in body mass and eventually 96–98% mortality (depending on the age class) and a quasi-extinction from which the population started to recover over the following years (Wilson & Peach 2006).

The collapse of the Leighton Moss population and the management of this population holds several crucial takeaways. First, changes in the population size can only be recognised if there is an adequate monitoring protocol in the population. The Leighton Moss population was subject to a systematic sampling of the individuals and their reproductive effort for over several years. The cryptic lifestyle of the reedlings, the lack of territories and their inhomogeneous breeding distribution make it challenging to estimate their abundance correctly (Hoi & Hoi 2001, Surmacki 2003, Surmacki & Stępniewski 2003, Vadász *et al.* 2011, Peiró 2013, Dadam *et al.* 2014, Malzer 2017). Systematic ringing and point counts from elevated observation points may yield adequate data, although the applicability of these methods may largely depend on the specific local circumstances and the timing of the census over the season and within a day (Trnka *et al.* 2006, Malzer 2017), and they are prone to the presence of transients in the population (Peiró 2017). Estimating breeding efforts directly may provide the most direct estimates of the nesting populations (Wawrzyniak & Sohns 1986, Wilson & Peach 2006), although this requires significant efforts due to the limited accessibility of nesting sites of the species. An alternative method could be the direct estimates of productivity based on captures of juveniles and using the iris colouration to indicate their age (Wilson & Hartley 2007).

Second, the temporary population collapse draws attention to the importance of food supplies, especially during winter flooding or large snow cover that may make the winter

seed reserves unavailable for the birds. As mentioned earlier, during the winter, the gut morphology of the reedlings adapts to a predominantly seed-based diet, which also requires the ingestion of small grit to facilitate the physical grinding of the food in the gizzard. An easy conservation management step that helps birds to find this useful resource is the installation of gritting platforms in the reed bed. Several of these platforms have been deployed in Leighton Moss, and the birds quickly adapted to them and used them regularly between September and December (Wilson 2014). These gritting trays also provide an ideal opportunity for a standardised collection of visual resighting of colour-ringed individuals that may alleviate the aforementioned difficulties with abundance estimation. Having the birds adapted to the gritting trays may also provide the opportunity to supplement the grit with seeds. Although this has not been reported for Bearded Reedlings, the effects of bird feeders on the winter survival of resident passerines is well known. Enriching the gritting trays or installing separate feeders may not affect the birds' survival under 'normal' conditions, but in case of a sudden drop in food availability, they may save the birds from starvation.

Another conservation intervention implemented in Leighton Moss is the installation of artificial 'nestboxes' made of reed (Wilson 2005). Depending on their location within the reed stand, the occupancy of these nestboxes may have reached 68% (Wilson 2015). Reed-based artificial nesting sites have been used for centuries in Central Europe. For instance, fishermen in Hungary used to break a bundle of reed stems and tie a knot from them to signal the location of their fish traps. As an eventual 'side-effect', these structures provided shelter and attracted various wetland species for nesting, including reedlings. Nowadays, these reed knots are explicitly used to provide additional nesting sites for reedlings (Kovács 1981, Fenyvesi 1999b).

A final and more complex consideration of the conservation of the species is the management of their habitat. As detailed above, Bearded Reedlings are highly specialised to reed-covered wetlands and are well-adapted to live in this habitat throughout their lifetime and exploit its resources. Therefore, the presence and breeding success of reedlings may provide insight into the condition and functioning of the wetland ecosystem as a whole (Malzer 2017). Since Bearded Reedlings are affected by different successional stages of reed stands (Beemster *et al.* 2010), efficient management of the reed for either economic harvesting or optimising between different needs of species in the wetlands requires careful planning. Cutting parts of the reed bed may have beneficial effects in terms of increased production, a more dense structure of the reed, and an increase in invertebrate biomass (Poulin & Lefebvre 2002). However, cutting the reed makes it unsuitable for reedlings as breeding sites, at least early in the season (Poulin & Lefebvre 2002, Vadász *et al.* 2008). Experience from the UK has shown biennial cutting (double wale) to be a good middle ground between conservation and commercial interests. However, in the Mediterranean region, the only viable long-term option seems to be a combination of annually cut and never cut reed patches. It is also possible that an optimal combination of cut and uncut reed patches could provide a similar conservation value to unmanaged reed beds (Poulin & Lefebvre 2002). Apart from cutting, appropriate management of water levels and water quality is also important (Peiró 2020).

It is unlikely that a wetland is only managed to protect Bearded Reedlings, therefore, the management strategy also needs to consider the potentially conflicting needs of different

target species (Malzer & West 2015, Wilson 2015). However, if conservation management aims to protect Bearded Reedlings in a given habitat, it can only be achieved efficiently if we take into consideration the intricate relationships between their life history, behaviour, physiology and their environment and synthesise the available information of this remarkable species. This review hopefully helps achieve this goal.

Acknowledgements

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