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Post-hatching testosterone concentration reflects nestling survival and pre-fledging offspring condition in the Tawny Owl *Strix aluco*

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We examined parental condition, brood sex composition, hatching order and post-hatching testosterone concentration in relation to nestling survival and pre-fledging offspring condition on Tawny Owls *Strix aluco* in Duna-Ipoly National Park, Hungary in 1996–2007. In smaller broods, where parents of poor condition suffered nestling mortality, hatchlings showed a male-biased sex ratio, and between-sibling differences in testosterone concentrations were high in the early nestling period. In broods where all nestlings were raised and parents were in good condition, hatchlings showed a female-biased sex ratio and between-sibling differences in testosterone concentrations were low. First- and second-hatched nestlings, with high post-hatching testosterone concentrations, survived after one or two siblings died and had better body condition before fledging than nestlings which fledged from the broods, where all were chicks raised.

1. Introduction

Hypotheses of brood reduction suggest that poor-quality parents would produce eggs that hatch more asynchronously than do eggs of good-quality parents, assuming constant clutch size, resulting in that the youngest offspring can be eliminated rapidly without the parents having to invest too much effort on their care (Gibbons 1987). The adaptive advantage of brood reduction increases if food becomes scarce, because earlier-hatched young may be fledged successfully without them having to compete with their later-hatched siblings (Lack 1954). Nevertheless, studies on sexually size-dimorphic bird species have shown that skewed sex ratios of offspring correspond with resource availability for parents, and that the larger sex, which is more costly to produce, is eliminated in conditions characterized by food scarcity. These phenomena have been documented for raptors (Olsen & Cockburn 1991, Arroyo 2002, Byholm *et al.* 2002), seabirds (Torres & Drummond 1999, Velando 2002) and songbirds (Paterson & Emlen 1980, Kilner 1998).

For Tawny Owls (*Strix aluco*), weather conditions affect prey availability to parents and therefore influence both the clutch size and the nestling survival during the breeding season (Southern & Lowe 1968, Wendland 1984, Saurola 1995, Solonen & Karhunen 2002, Solonen 2004, 2005). The reproductive performance and parental condition of Tawny Owls vary between years according to weather conditions (Sasvári *et al.* 2004, Sasvári & Hegyi 2005). Both males and females weigh less in adverse weather when snow covered the ground, but were heavier in breeding years without snow cover (Sasvári *et al.* 2000, 2004). Moreover, broods show a male-biased sex ratio during years with adverse conditions, but a female-biased sex ratio in more favorable conditions (Sasvári & Nishiumi 2005). In adverse conditions, female nestlings are more likely to die before fledging than male nestlings.

The post-hatching effects of yolk steroid hormones on between-sibling variation in offspring survival have been reported both for passerines and non-passerines (Schwabl 1996, Lipar & Ketterson 2000, Eising *et al.* 2001). Maternal hormones affect the offspring testosterone concentration in the early nestling period (Sasvári *et al.* 2005). White Stork (*Ciconia ciconia*) and Tawny Owl hatching order and testosterone levels correlate negatively in adverse but not in favorable conditions (Sasvári *et al.* 1999, 2004). In adverse conditions, the parents suffer elevated nestling mortality, but in more favorable conditions nestlings are usually raised successfully.

Natural selection maximizes the number of recruits to the breeding population rather than the number of nestlings (Smith & Fretwell 1974, Brockelman 1975). Hence, we hypothesise that the lower number of offspring in adverse years, compared with total broods, is compensated by increased survival of fledglings. On the basis of the brood-reduction hypothesis (Lack 1954, Gibbons 1987), and the different relationships in testosterone levels and hatching order between broods raised in adverse and favorable conditions (Sasvári *et al.* 1999, 2004), we presumed that post-hatching testosterone concentration influences the nestling survival and reflects the survival chances of fledglings. To test these assumptions, we set nest boxes for Tawny Owls for over 12 years and, similarly to our earlier studies, evaluated parental and offspring conditions based on body weight (Sasvári *et al.* 2004, Sasvári & Hegyi 2005). The Tawny Owl is a resident, sexually dimorphic, monogamous species. Females and chicks are fed by the (smaller) males during the incubation and brooding periods. We related the survival rate of chicks to their hatching order and testosterone concentrations measured in early nestling period. The pre-fledging body conditions of young were evaluated in relation to the number of siblings leaving nests. In addition, the relationship between testosterone levels and nestling survival were evaluated separately for male and female offspring.

We put forward three questions: (1) Are the post-hatching testosterone levels related to nestling survival and offspring condition before fledging? (2) Do the parents improve the survival chances of some fledglings at the cost of others? (3) Are there sex-related differences in the relationships in the post-hatching testosterone levels and nestling survival?

2. Material and methods

2.1. Study area and sample size

Between 1996 and 2007, two hundred and twenty nest boxes for Tawny Owls were placed in 40–60-years old mixed oak/hornbeam/beech forest, within the Duna-Ipoly National Park 30 km northwest of Budapest, Hungary (47°35' N, 19°02' E). Field work and blood-sample collecting were carried out in cooperation with the management of Duna-Ipoly National Park (the authority for Nature Conservation within the study area). Groups of 6–8 nest boxes were placed 300–600 m apart, the groups in turn being 2–5 km apart. As the earliest clutches are laid in February, nest-boxes were checked at 4–8-day intervals from the end of January. Owl parents were captured by placing a net over the entrance of the box while the birds were inside, and the birds were marked with different combinations of color rings to ensure individual identification. Tawny Owl is sexually size dimorphic; hence, females and males could be distinguished by weight.

A total of 151 females and 133 males were captured and marked during the study period. Of these 284 individuals, 60 pairs (5.00 ± 1.10 SD, range 4–6 pairs/year) produced three nestlings for whom hatching order could be determined, and all represented different individuals; these pairs and their offspring were thus chosen to study. Nests with eggs were checked at 3–4-day intervals and, as the mean interval between first- and third-hatched nestlings was 2.87 ± 0.34 SD days ($n = 60$), the hatching order could be determined by body size and body weight.

Hatching order of the owlets was indicated by color painted on tarsi. Weight and sex of parents and owlets, offspring survival, and plasma testosterone concentrations of the nestlings were analyzed. Parents were weighed when nestlings were 3–5 days old, and nestlings were weighed when they were 25–26 days old. Evaluation of data was based on a comparison between broods with a mortality of 1–2 nestlings and broods with no mortality. Field work and blood sampling did not cause mortality or otherwise negatively affect the nestlings.

2.2. Analysis of testosterone concentration

The majority of nestlings suffering mortality died between 3 and 10 days after hatching (83.7% of 43 individuals; $\chi^2 = 39.1$, $P < 0.001$). Hence, blood samples (50–100 ml) were collected from the nestlings by brachial venipuncture when they were 3 days old. In order to avoid the normal daily fluctuation in testosterone level, blood samples were always collected at 10.00 and 12.00 AM. Blood was drawn into heparinized polyethylene tubes and stored in a cooler. After centrifugation, the plasma was immediately stored in a deep freezer at –20°C. Plasma samples (10–50ml) were extracted with 10 volumes of diethyl-ether three times, with a 30-min extraction time. Testosterone concentrations were analyzed, without chromatography, by radioimmunoassay (RIA; Péczely *et al.* 1980). The detection limit was 5 pg/assay tubes. Intra- and inter-assay differences were 8% and 11%, respectively.

The antibody cross-reacts with 5-α-dihydrotestosterone at a level of 40%, but since the known concentration of this androgen in the avian plasma is generally less than 10% (Galli *et al.* 1973, Rissman & Wingfield 1984), it probably only slightly affects the testosterone concentration. The existence of other, probably less potent, androgens (androstenedione, dehydroandrosterone and dehydroandrosterone sulphata) cannot be excluded but their cross-reaction with the used antibody is less than 1% (Péczely *et al.* 1980).

2.3. Determination of sex

The sex of 180 nestlings was analyzed using a molecular method developed by Ellegren (1996). DNA was extracted from blood samples preserved in pure ethanol by phenol/chloroform. Polymerase chain reactions (PCRs) were conducted using three primers, 2945F, cfR and 3224R (Ellegren 1996). The PCR products were subjected to electrophoresis in 1.5% agarose gels with ethidium bromide in 1xTAE buffer for 20 minutes at 100V and visualized under UV illumination. A single band of 630 bp, present in all individuals, acts as a positive control of PCR reactions. A stronger band of 210 bp, present only in some individuals, indicated that they were females.

In order to verify the reliability of sexing of the Tawny Owls using the method of Ellegren (1996), we reanalyzed 20 individuals (10 for each of the suggested males and females) using primer sets P2 and P8, designed by Griffiths *et al.* (1998), which detect the difference in length between W-linked and Z-linked CHD gene fragments, depending on the intron. The PCR products were electrophoresed in 3.0% agarose gels for 100 minutes. A fragment of ca. 370 bp was present in all individuals, but the fragment of about 380 bp was present only in those individuals considered to be females by the Ellegren method. We thus obtained the same results for all 20 individuals with both methods, suggesting that both methods are reliable for sexing Tawny Owls.

2.4. Statistical analyses

The relationships between complete and reduced broods, the condition of their parent (assigned as ‘good’ or ‘bad’ dependent on body weight) and with nestling sex ratios, were evaluated using chi-square statistics with 50:50 being the expected ratio. ANOVA was performed to analyze the between-sibling differences in testosterone concentrations. Also, ANOVA was used to examine the

Table 1. Body weight of Tawny Owl parents in relation to survival of their nestlings. In parentheses, number of parents.

Survival/Mortality of nestlings	Parent weight (g ± SD)	
	Males	Females
Second- and third-hatched died	351.8 ± 23.0 (15)	414.7 ±17.0 (15)
Third-hatched died	370.2 ± 26.0 (18)	430.2 ± 22.3 (18)
All nestlings (three) fledged	431.0 ± 20.4 (27)	492.0 ± 19.3 (27)

relationships between the pre-fledging condition and sibling mortality of nestlings and between pre-fledging tarsal length and sibling mortality. Multiple logistic regression was used for modeling the effects of testosterone concentration, hatching order, gender and brood mortality on nestling survival (Cox & Snell 1989). All statistical tests were done using SPSS (Norusis 1994).

3. Results

3.1. Parental condition and sex ratio affecting the broods

Offspring ($n = 180$) were more likely to survive the nestling period when they hatched in the nests of parents in good condition (i.e., heavier individuals): complete broods were raised when both parents had high body weight (all 81 of 81 chicks), but only one offspring fledged from nests of parents with the lowest body weights (15 of 45 chicks; $\chi^2_2 = 6.0$, $P < 0.05$; Table 1). In reduced broods, first-hatched nestlings always fledged (33 chicks) but by definition all third-hatched nestlings died (33 chicks). In reduced broods where one or two later-hatched nestlings died, the first-hatched nestlings were male biased (24 of 33 chicks). However, in broods where hatchlings were raised by parents in good condition, the majority of first-hatched offspring were females (17 of 27 chicks), reflecting a reverse sex ratio ($\chi^2_1 = 7.6$, $P < 0.01$; Fig. 1). There were no significant differences in sex ratios between reduced and complete broods either in second-hatched (19 and 11 males of 33 and 27 chicks, respectively; $\chi^2_1 = 1.2$, n.s.) or third-hatched nestlings (16 and 13 males of 33 and 27 chicks, respectively; $\chi^2_1 = 0.1$, n.s.). When all hatchlings were pooled, they showed a similar sex ratio as did the

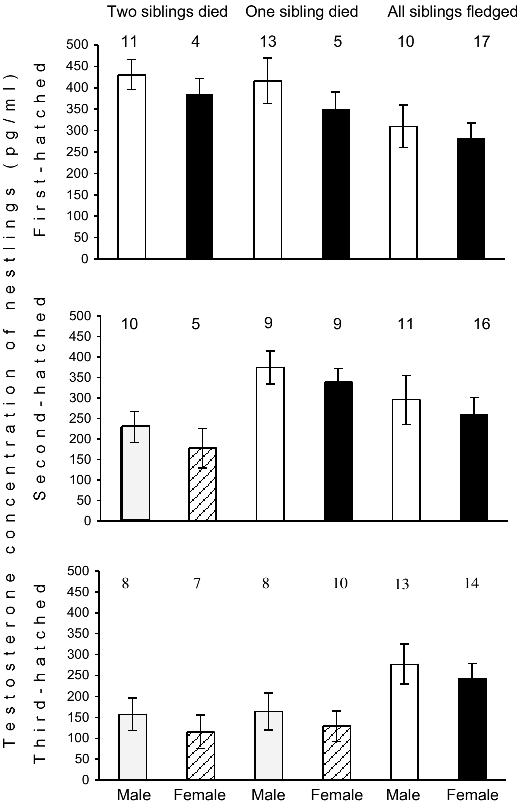

Fig. 1. Testosterone concentration (pg/ml ± SD) of male and female nestlings in relation to hatching order in the broods of Tawny Owls where either one or two siblings died or all siblings survived. First, second and third rows of columns indicate first-, second- and third-hatched nestlings. Open and black columns indicate male and female nestlings that fledged; dotted and hatched columns indicate males and females that died before fledging. Numbers above the columns indicate numbers of nestlings. Sample size for broods where 1–2 siblings died or all siblings fledged were 18, 15 and 27, respectively.

Table 2. Logistic regression for nestling survival: effects of post-hatching testosterone concentration, hatching order, gender and brood mortality. Plasma testosterone concentrations (pg/ml) were analyzed from blood samples collected from three days old nestlings. Hatching order was divided into three: first-, second- or third-hatched nestlings, gender was either male or female, and brood mortality was divided into three: all three nestlings fledged, one of the three nestlings died, or two of the three nestlings died, before fledging.

	Chi-square	df	P	Regr. coeff. (B)	SE of B
Testosterone concentration	9.16	1	0.003	0.048	0.014
Hatching order	6.55	1	0.012	–0.037	0.017
Gender	4.73	1	0.039	–0.011	0.009
Brood mortality	4.84	1	0.036	0.024	0.011

reduced and complete broods (59 and 34 males of 99 and 81 chicks, respectively; $\chi^2_1 = 5.5$, $P < 0.02$).

3.2. Testosterone concentration in nestlings

In reduced broods, nestlings had high between-sibling differences in testosterone levels: the concentrations were significantly higher in first-hatched chicks that all survived the nestling period than in third-hatched owlets that all died ($F_{2,96} = 7.27$, $P < 0.001$; Fig. 1). However, in complete broods (all young fledged), lower between-sibling differences were recorded ($F_{2,78} = 3.16$, $P = 0.043$). Testosterone concentrations of first-hatched nestlings in reduced broods were higher than those of first-hatched nestlings of all broods ($F_{1,58} = 9.33$, $P < 0.001$). Third-hatched nestlings that died in reduced broods had lower testosterone concentrations than the surviving third-hatched chicks of all broods ($F_{1,58} = 9.19$, $P < 0.001$). Generally, testosterone concentrations were higher in males than in females ($F_{1,178} = 3.71$, $P < 0.027$).

The multiple regression revealed that both male and female offspring with high testosterone

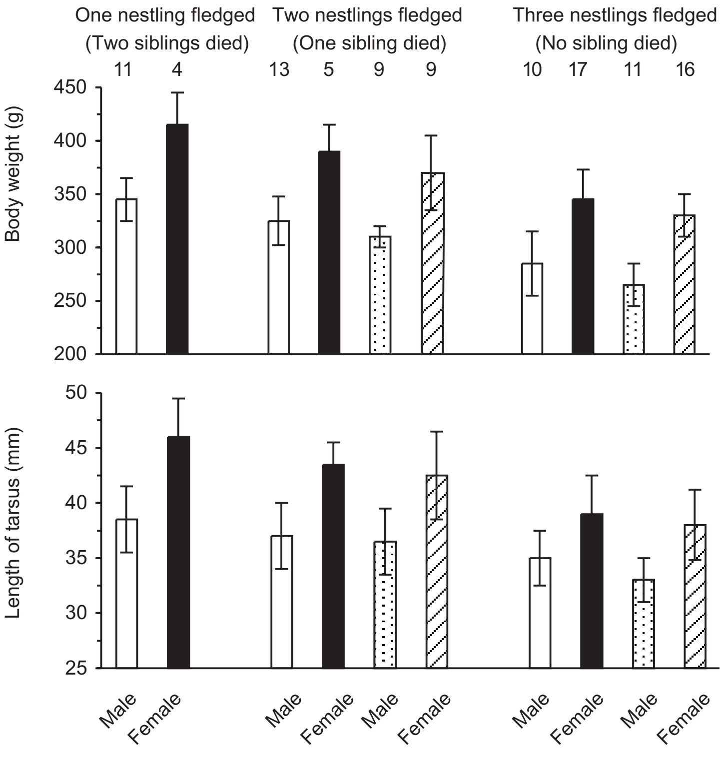

Fig. 2. Body weight (g ± SD) and length of tarsus (mm ± SD) for male and female nestlings before fledging in relation to sibling survival and hatching order. Open and black columns indicate first-hatched male and female nestlings, hatched and dotted columns indicate second-hatched male and female nestlings. Numbers above the columns indicate numbers of nestlings.

concentrations were more likely to survive the nestling period than offspring with low testosterone level (Table 2). Later hatching order reduced the likelihood of survival, and brood mortality was linked to higher death rates in female than in male nestlings.

3.3. Conditions of first- and second-hatched nestlings before fledging

For both males and females, body weights of first-hatched nestlings with sibling mortalities of 1–2 were heavier than first-hatched nestlings that fledged with two siblings (males: $F_{2,31} = 6.72$, $P = 0.003$ and females: $F_{2,28} = 6.44$, $P = 0.005$; Fig. 2). Moreover, first-hatched individuals that fledged alone or with one sibling had longer tarsi than first-hatched nestlings that fledged with two siblings (males: $F_{2,31} = 5.23$, $P = 0.014$ and females: $F_{2,23} = 5.60$, $P = 0.011$).

For both males and females, second-hatched nestlings that fledged with one sibling were heavier and had longer tarsi than first-hatched nestlings that fledged with two siblings (weight, males: $\mathrm{F}_{1,17} = 5.87$, $P = 0.027$ and females: $\mathrm{F}_{1,24} = 4.80$, $P = 0.035$; tarsus length, males: $\mathrm{F}_{1,17} = 5.34$, $P = 0.033$ and females: $\mathrm{F}_{1,24} = 5.14$, $P = 0.029$). These nestlings were also heavier and had longer tarsi than second-hatched nestlings that fledged with two siblings (weight, males: $\mathrm{F}_{1,18} = 11.29$, $P = 0.002$ and females: $\mathrm{F}_{1,23} = 9.31$, $P = 0.007$; tarsus length, males: $\mathrm{F}_{1,18} = 7.15$, $P = 0.017$ and females: $\mathrm{F}_{1,23} = 7.69$, $P = 0.011$). Nestlings that fledged alone, i.e., without siblings, had the highest body weight and tarsus length among all nestlings that fledged with one or two siblings (weight, males: $\mathrm{F}_{2,51} = 7.16$, $P < 0.001$ and females: $\mathrm{F}_{2,48} = 5.93$, $P = 0.004$; tarsus length, males: $\mathrm{F}_{2,51} = 5.44$, $P = 0.006$ and females: $\mathrm{F}_{2,48} = 5.04$, $P = 0.009$).

4. Discussion

4.1. Male-biased survival of offspring with high post-hatching testosterone levels in reduced broods

Tawny Owl mothers of poor condition produced nestlings with high between-sibling differences in testosterone levels. The first-hatched offspring, most of whom were males, had the highest concentrations, and all survived the nestling period. The first-hatched female nestlings in these reduced broods had lower testosterone levels than the first-hatched males, but these were higher than the concentrations of all later-hatched offspring, including males. All third-hatched chicks that died had the lowest levels of testosterone. In the broods where all nestlings were raised by parents in good condition, the sex ratio was female biased and the between-sibling variation in testosterone concentration was low.

Higher testosterone concentration evokes increased locomotor activity (Wada 1986, Massa & Bottomi 1987), aggression (Wingfield *et al.* 1990, Beletsky *et al.* 1990) and interactions between offspring and their parents (Andrew 1975). Eising and Groothuis (2003) showed that, for the Black-headed Gull (*Larus ridibundus*) eggs that were injected with a mixture of testosterone and androstenedione, produced chicks that begged more frequently and obtained a larger share of food than did chicks hatching from eggs injected with sterile sesame oil.

For the first-hatched chicks of reduced broods in the White Stork, chicks with higher testosterone level responded quicker to the feeding parents and were more likely to be fed first than chicks with lower testosterone level (Sasvári *et al.* 1999). The later-hatched stork chicks that suffered nestling mortality, never received food first. The particularly high testosterone concentration in the first-hatched male Tawny Owl nestlings may have produced this type of behavior. The later-hatched siblings, with low testosterone concentrations, may have exhibited a weaker response to the feeding females and consequently received less food.

4.2. Surviving nestlings improve their condition before fledging at the cost of their siblings

Both male and female first-hatched nestlings fledged with higher body weight and longer tarsi when fledged with 0–1 siblings than they did when fledged with two siblings. Similarly, the second-hatched nestlings were in better condition when fledged with one sibling than with two. The single-fledged offspring were in the best condition, indicating that they benefited most from the deaths of both their siblings.

Raptor fledglings are threatened both by predation and starvation and suffer high mortality after leaving their nests (McFadzen & Marzluff 1996, Rohner & Hunter 1996). Overskaug et al. (1999) carried out telemetry studies on Tawny Owl fledglings at the northern limit of the range of this species and found a 61% mortality rate before dispersal. Overskaug *et al.* (1999) confirmed that fledglings in good condition had a higher chance for surviving: offspring that died or disappeared during the first ten days after leaving the nest were lighter than those that were still alive at that time. Based on these findings, the heavier nestlings may have been more likely to survive after fledging in the present study area.

Studies on both passerines (Tinbergen & Boerlijst 1990, Lindén *et al.* 1992) and non-passerines (Coulson & Porter 1985, Newton 1989) have shown that the survival of fledglings depends on body size and weight. However, offspring weight decreases with increasing brood size (Korpimäki & Rita 1996, Sanz & Tinbergen 1999). These observations are supported by the present findings that, in reduced Tawny Owl broods, the number of siblings dying and the condition of nestlings that survived to fledge, were positively associated.

4.3. Conclusions on environmental impact

Lundberg (1986) and Korpimäki (1986) suggested that the reversed sexual dimorphism in owls has evolved as a result of selection for heavier females to allow them to resist starvation. The advantage of larger females is an increased ability to store energy during periods of food shortage. The smaller, lighter adult males with shorter wings are more efficient hunters, but less resistant to starvation and suffer higher mortality than adult females during severe winter conditions (Mueller 1989, Sunde *et al.* 2003). The present study confirmed that, in broods of the sexually dimorphic Tawny Owl, the raising of smaller sons, requiring less provision, is favored in reduced broods. Moreover, less parental investment is required to produce sons with good condition before fledging, than daughters. Parents compensate for the decrease in offspring number by ensuring a higher probabilty of survival to independence for offspring that successfully fledge from the nest.

In the local population studied, adult males were more likely to have disappeared (died?) after a winter with more snowy days, whereas the rate of adult female disappearance (death rate?) was not affected by weather (Sasvári & Nishiumi 2005). As the fledglings in the present study were male biased during adverse conditions but female biased during favorable conditions, the adjustment of sex ratio to weather conditions has important implications for the demography of breeding populations of the Tawny Owl. However, Desfor *et al.* (2007) found for Danish Tawny Owls that brood sex ratios were not correlated with resource abundance and there was no male-biased sex skewing following food shortage during the nestling period. Desfor *et al.* (2007) suggested that the inconsistency in the sex ratio allocation between populations may be due to different adaptive strategies of parents adjusting to different reproductive constraints.

When food conditions are poor, mother Tawny Owls may deposit highly variable testosterone levels into the yolk, thus increasing the chance of survival by producing high concentrations in the first-hatched eggs from which male offspring are born. Mothers in good condition, on the other hand, may deposit almost equal testosterone concentrations in every egg, and the proportion of males declines in broods where all nestlings fledge. This interpretation supports the concept of relationships between hormonal brood-size control and foraging ability of parents and/or the availability of food resources (Royle *et al.* 2001). The present findings demonstrate the need for cross-taxonomic surveys on the functioning of maternal hormones in reproductive optimisation, including the effects of environmental factors on endocrine control.

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Kuoriutumisen jälkeinen testosteronitaso heijastaa poikasen selviytyvyyttä ja lentopoikasvaiheen kuntoa lehtopöllöllä

Tutkimme vanhempien kunnon sekä poikueen sukupuolijakauman, kuoriutumisjärjestyksen sekä elimistön kuoriutumisvaiheen testosteronipitoisuuden suhteita poikasten selviytyvyyteen ja lentopoikasvaiheen kuntoon lehtopöllöllä (*Strix aluco*) Duna-Ipolyn kansallispuistossa Unkarissa 1996–2007. Kuolevuuden takia pienentyneissä poikueissa, joita kasvattivat huonokuntoiset vanhemmat, vastakuoriutuneiden poikasten sukupuolijakauma oli koiraspainotteinen, ja pesyeen sisäinen vaihtelu testosteronitasossa oli suurta varhaisessa pesäpoikasvaiheessa.

Hyväkuntoisten vanhempien sellaisissa poikueissa, joista varttuivat kaikki poikaset, sukupuolijakauma oli naaraspainotteinen ja poikueen sisäiset testosteronipitoisuuksien erot pieniä. Ne ensimmäisenä ja toisena kuoriutuneet poikaset, joiden testosteronitaso oli korkea mutta joiden sisaruksista yksi tai kaksi kuoli pesäpoikasvaiheessa, olivat parempikuntoisia kuin yhteenlaskien ne poikaset, jotka varttuivat lentopoikasiksi pesissä, joista kaikki poikaset selviytyivät. Vanhemmat saattavat kompensoida alentunutta lentopoikasten määrää pyrkimällä varmistamaan vähempien poikasten selviytyvyyden pesä- ja lentopoikasvaiheiden yli.

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