

# Long-term increase in female body condition and its effect on reproduction in two European red-listed species, Common Pochard (*Aythya ferina*) and Tufted Duck (*Aythya fuligula*)

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Body condition of breeding females is an important driver of an individual's fitness and the consequent dynamics of populations. Long-term changes in female body condition are likely to be affected by recent shifts in climatic and environmental conditions that can result in changes to population demography. To help explain the drivers shaping body condition during the incubation period and its consequences for reproductive success, we examined the long-term pattern in the body condition of breeding females of two declining sympatric diving duck species: Common Pochard *Aythya ferina* and Tufted Duck *Aythya fuligula*. We analysed the data obtained from 139 females of Common Pochard and 251 females of Tufted Duck breeding on fishponds in South Bohemia, Czechia, between 2004 and 2020. We calculated the body condition index of females during late incubation based on the residuals from the relationship between body mass and tarsus length and used the incubation stage as an additional predictor of body mass. Body condition of both species did not decline over the 17 years of the study. The effect of winter weather conditions (winter temperature), water transparency (a proxy for food availability) and reproductive investment on body condition was not confirmed. Female body condition positively affected mean egg mass and hatchability in both studied species, i.e. females in better body condition laid larger eggs and hatched eggs with a higher hatching probability. We conclude that the population declines of the studied species are probably not connected to decreasing body condition of breeding females, but other reasons such as change in breeding propensity or offspring survival and recruitment should be considered in future studies.

Tělesná kondice hnízdících samic je považována za důležitou individuální charakteristiku, která ovlivňuje fitness jedinců a populační dynamiku jednotlivých druhů. Dlouhodobé změny v tělesné kondici mohou být důsledkem působení klimatických a environmentálních podmínek na jedince, a následně mohou mít vliv na demografii a přežívání populací. V naší studii jsme analyzovali vliv faktorů prostředí na tělesnou kondici inkubujících samic a vliv tělesné kondice na parametry reprodukce u dvou druhů potápivých kachen – poláka velkého *Aythya ferina* a poláka chocholačky *Aythya fuligula*, u nichž je recentně v Evropě dokládán pokles početnosti. U těchto druhů jsme hodnotili dlouhodobý trend jejich tělesné kondice a parametrů reprodukce. Celkově byla

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analyzována data pro 139 samic poláka velkého a 251 samic poláka chocholačky hnízdících na rybníčních lokalitách v jižních Čechách (ČR) v letech 2004–2020. Pro vyjádření tělesné kondice studovaných jedinců byl stanoven index tělesné kondice na základě tělesné hmotnosti a délky tarsu hnízdících samic zjišťovaných v pozdní fázi inkubace. Jako další prediktor poklesu tělesné hmotnosti v průběhu inkubace byl do výpočtu kondičního indexu individuální samice zahrnut počet dní do líhnutí. Na základě výsledků získaných v průběhu 17 let nedochází k poklesu kondice inkubujících samic. Vliv podmínek předchozí zimy, průhlednosti vody a investice do reprodukce na tělesnou kondici hnízdících samic nebyl prokázán. Byl zjištěn signifikantní vliv tělesné kondice na průměrnou velikost vejce ve snůšce u obou studovaných druhů. Tělesná kondice studovaných druhů pozitivně ovlivňovala také úspěšnost líhnutí. Z výsledků studie vyplývá, že pokles populací obou druhů pravděpodobně nelze vysvětlit dlouhodobým poklesem kondice hnízdících samic. Kondice hnízdících samic naopak narůstá a pozitivně ovlivňuje i některé hnízdící parametry. Pro další zhodnocení možných příčin poklesu početnosti evropských populací studovaných druhů potápivých kachen by bylo vhodné analyzovat změny v proporcii hnízdících samic v populacích, stejně jako faktory ovlivňující přežívání mláďat a jejich úspěšný vývoj do dospělosti.

**Keywords:** body condition index, climate change, diving ducks, egg mass, hatchability.

Study of the drivers shaping female body condition and the subsequent relationship between body condition and reproductive success is essential for understanding the population dynamics of a species and/or the species' ability to face a changing environment (Blums *et al.* 2005, Guillemain *et al.* 2010, English *et al.* 2018), especially for large-bodied species such as waterfowl. This is particularly relevant when evaluating the causes and consequences of population change in species in decline and designing subsequent conservation measures (Anteau & Afton 2004).

Body condition is regarded as an indicator of the health and physiological properties of an individual and is influenced by a combination of factors (Schluter & Gustafsson 1993, Klimas *et al.* 2020). Generally, low food supply (Delnicki & Reinecke 1986, Anteau & Afton 2008), disturbance or unfavourable weather conditions (Janke *et al.* 2019), reproductive status, parasitic and infectious diseases (Arsnoe *et al.* 2011), high predation pressure, and high inter- and intraspecific competition are considered the most critical factors resulting in deteriorating body condition of breeding females (Birkhead *et al.* 1983, Devries *et al.* 2008). Furthermore, feeding conditions at one stage of the annual cycle can affect the performance of migrating birds at a later stage, as has been shown for numerous species of ducks (Arzel *et al.* 2006, Drent 2006, Newton 2007, Sedinger & Alisauskas 2014). For example, feeding

conditions in the wintering areas can influence subsequent breeding success, and spring/summer conditions can influence subsequent overwintering survival. These factors cause carry-over effects on individuals, influencing individual survival and reproduction, and have been revealed as cross-seasonal effects on the breeding populations and their dynamics (Devries *et al.* 2008, Guillemain *et al.* 2008, Newton 2013, Sedinger & Alisauskas 2014, Podhrázský *et al.* 2017).

In recent decades, climate warming has considerably increased the availability of wetlands suitable for wintering waterbirds (Maclean *et al.* 2008, Thomas *et al.* 2012, Pavón-Jordán *et al.* 2015, Musilová *et al.* 2018, Pavón-Jordán *et al.* 2019). Some species are responding to this phenomenon by altering their migratory behaviour (Sauter *et al.* 2010, Gunnarsson *et al.* 2012, Adam *et al.* 2015). For example, long-term climate warming (Hurrell & Deser 2010) has allowed some species to extend the length of the breeding season (Halupka *et al.* 2008, Lv *et al.* 2020), shorten their migration distance (Sauter *et al.* 2010) and alter the time of arrival from wintering grounds (Hüppop & Hüppop 2003, Podhrázský *et al.* 2017). In the temperate zone, an earlier arrival to the breeding grounds can allow breeders to acquire a greater amount of nutrients for clutch formation during pre-breeding periods (Drent & Daan 1980, Bêty *et al.* 2003) and hence restore their body condition after spring migration

to the breeding areas. Hence, waterbirds' body condition is also expected to change (Guillemain *et al.* 2010), linked to these observed phenological/behavioural responses to climate change. In addition to the direct climate-driven changes in body condition, climate change also alters the conditions of wetland habitats (Moss *et al.* 2011).

Fishponds represent an important breeding habitat for waterbirds, especially diving ducks (Broyer & Bourguemestre 2020). Changes in the food web structure of fishponds are related to the high density of stocked fish, especially Carp *Cyprinus carpio*. The low water transparency (overloading of organic matter, bloom of phytoplankton, low density of invertebrates) of fishponds indicates a poor trophic status (Šimek *et al.* 2019). In the Czech Republic, fishponds are the main breeding habitat for waterbird species. The low food availability for waterbirds often found in these ponds is associated with the current intensive management of fishponds in central Europe, which could result into lower body condition of breeding females at a later stage in the annual cycle (Behney 2020).

Body condition – as a qualitative assessment of a bird health – is directly related to its Darwinian fitness. Breeding duck females in poor body condition may delay the onset of breeding (Öst *et al.* 2011) due to a lack of nutrients (especially lipids and proteins) that are allocated to reproduction (Drobney & Fredrickson 1985, Ankney & Afton 1988, Descamps *et al.* 2011) in contrast to nutrients required for self-maintenance (Williams 2008). The need for appropriate replenishment of nutrients for breeding in individuals with poor body condition is time-consuming and reduces the opportunity for reneating and finding a suitable feeding habitat for ducklings, and/or shortens the female care period of rearing ducklings (Sedinger & Raveling 1986, Paasivaara & Pöysä 2007, Both *et al.* 2010, Reséndiz-Infante & Gauthier 2020). Hence, body condition is directly linked to individual productivity and fitness.

Ducks are an ideal group for studying alterations in body condition due to their large body size, high visibility and marking possibilities compared with smaller birds. Yet, comparative studies on duck body condition and reproductive success in the Palaearctic are scarce compared with those in the Nearctic (Barboza & Jorde 2002, Devries *et al.* 2008, English *et al.* 2018).

This paper aims (i) to assess changes over time in female body condition of two declining diving

duck species, Common Pochard *Aythya ferina* and Tufted Duck *Aythya fuligula*, in a 17-year study, and (ii) to gain a better understanding of the relationship between female body condition and breeding success. These sympatric and congeneric diving duck species use the same breeding habitat, and are precocial and benthophagous, feeding primarily on invertebrates during the breeding season (Snow & Perrins 1998, Kear 2005, Štátný & Hudec 2016), but differ in body size, timing of breeding, and egg and clutch size (Kear 2005).

Based on current knowledge concerning long-term climate warming (Hurrell & Deser 2010) that could result in lower energetic costs for wintering birds in recent decades (Sauter *et al.* 2010, Gunnarsson *et al.* 2012, Adam *et al.* 2015), and the velocity of the changes in climatic conditions and species' responses (Parmesan & Yohe 2003, Chen *et al.* 2011, Pacifici *et al.* 2015), we hypothesized an increasing positive effect of drivers of body condition acting *prior* to nesting (winter temperature) as opposed to drivers acting *at the time* of nesting (water transparency) over the study period. This assumption is highly relevant in view of the capital–income breeding dichotomy (Drent & Daan 1980, Janke *et al.* 2015). Waterfowl in general are expected to be partial capital breeders, with little evidence for temperate-nesting species, which rely on a combination of stored and locally acquired nutrients for clutch formation and incubation (Alisauskas & Ankney 1992, Guillemain *et al.* 2008) at arrival in breeding areas. Under increasingly favourable wintering conditions acting prior to nesting, we expected a long-term improvement in female body condition, especially in breeding seasons after milder winters (Lehikoinen *et al.* 2006).

Regarding the body condition–reproductive performance relationship (Bêty *et al.* 2003, Warren *et al.* 2014, Folliot *et al.* 2017), body condition acts as a key predictor of the reproductive performance (laying date, egg mass, clutch size and hatchability). Given the high energetic costs of reproduction (Owen & Black 1990), we expected a lower body condition of breeding females immediately after a higher reproductive investment (expressed by loss of body condition as a nutritional investment in clutch formation and egg incubation). We also hypothesized that females in better late-incubating body condition would have an earlier laying date, higher egg mass, larger clutch size and higher hatchability (Blums

*et al.* 1997) compared with females with lower body condition. This variation in body condition will also be reflected in long-term changes in breeding performance. Allocation of stored body nutrition limits clutch formation (Bengtson 1971, Pehrsson 1991, Eichholz & Sedinger 1999), and hence we predicted that higher values of body condition would be associated with the laying of larger eggs (expressed as mean egg mass) and/or with the laying of larger clutches (expressed as total clutch size/non-parasitized clutch size). Regarding the benefits of early breeding, we expected females in better body condition to breed earlier in the season (Blums *et al.* 2005, Devries *et al.* 2008).

## METHODS

### Study area

The field data were sampled on 173 fishponds in the Třeboň Biosphere Reserve and surrounding area in South Bohemia, Czech Republic (48.97–49.26°N, 14.66–14.97°E) between 2004 and 2020. Fishponds are permanent, shallow and eutrophic waterbodies with a small stream or canal for water inflow and represent the most common wetland type in the study area as well as in the Czech Republic. As commercial subjects aimed at stocking and production of fish (mostly Carp), fishponds were formed in the Middle Ages (mostly in the 16th century) with artificially managed water levels, chemistry and nutrient input (Musil 2006, Musilová *et al.* 2021). The water surface area of the observed fishponds varied between 0.21 and 298.00 ha (mean  $\pm$  sd = 16.97  $\pm$  39.82 ha) and the proportion of cover of emergent vegetation varied between 1.03% and 90.0% (mean  $\pm$  sd = 21.30  $\pm$  16.26%). Most of the emergent vegetation, namely Common Reed *Phragmites australis*, Cattail *Typha latifolia*, sedges *Carex* spp., Great Manna Grass *Glyceria maxima* and willows *Salix* spp. (Janda *et al.* 1996, Čehovská *et al.* 2019), was located along shorelines or in the shallow water centres of fishponds.

### Nest survey and catching females

Nest surveys were performed by slow walking, and systematically and carefully searching in vegetation on islands and in the emergent vegetation of fishponds with constant monitoring effort (Čehovská

*et al.* 2019). All eggs in each observed nest were numbered, measured in length and width to the nearest 0.1 mm using a digital calliper, and their colour and shape were recorded (to exclude parasitic eggs, see Dugger & Blums 2001). We identified 106 (5.4%) parasitic eggs in 40 (20.6%) clutches of Common Pochard and 115 (3.4%) in 44 (13.7%) clutches of Tufted Duck. Incubation stage of clutches was estimated using a flotation technique (Westerskov 1950) and candling (Weller 1956) during regular visits of the nests and corrected according to hatching date and the last egg-laying date. Breeding females of Common Pochard and Tufted Duck were caught on their nests in the late incubation stage using drop-door traps (Weller 1957). Incubation stage at capture did not change significantly over the study period (Common Pochard:  $r = -0.045$ ,  $P = 0.533$ ,  $n = 194$ ; Tufted Duck:  $r = -0.006$ ,  $P = 0.908$ ,  $n = 322$ ). Clutch size was obtained based on total egg count (total clutch size; maximum number of eggs present in the nest) and after subtracting number of eggs considered as parasitic (non-parasitized clutch size; maximum number of non-parasitic eggs present in the nest). There was only one record of re-nesting in the study period, which was excluded from the data analyses. Each captured female was transported in a cloth bag to the shore of a fishpond where the female was weighed using a spring balance while settled in a cotton bag. Immediately after removal from the bag, the tarsus length of each female was taken using a steel rule and digital callipers (see Table 1). Ducks were released immediately after weighing, measuring and marking with individually coded nasal saddles and combinations of colour rings on legs.

### Biotic and abiotic variables

We selected biotic and abiotic variables that could directly influence female body condition and/or drivers that could cause carry-over effects on body condition of an individual through habitat quality at the wintering and breeding areas (Sedinger & Alisauskas 2014, Folliot *et al.* 2017). First, as an indicator of preceding winter conditions and food availability at the arrival site we used *winter temperature* and *water transparency*, respectively. *Winter temperature* was obtained as monthly averages (December, January, February) for the temperatures of the most important wintering areas of the studied species covered by the 50% kernel density

**Table 1.** Body mass, tarsus length and body condition index (the residuals from the regression of the log of mass (g) on (1) the log of tarsus length (cm) and (2) the incubation stage) of Common Pochard and Tufted Duck females (all records).

	Common Pochard ( <i>n</i> = 194)		Tufted Duck ( <i>n</i> = 322)	
	Mean ± sd	Range	Mean ± sd	Range
Body mass (g)	773.4 ± 37.4	660–865	614.0 ± 46.1	490–880
Tarsus length (mm)	39.34 ± 1.95	33.5–48.4	34.9 ± 2.25	24.5–43.4
Body condition index	0.185 ± 4.73	–9.504 to 9.834	0.047 ± 4.78	–9.958 to 9.994

of the females' (marked with nasal saddle and recorded as living) recoveries (ESRI 2016, Sussman *et al.* 2019). *Water transparency* is the transparency of water measured with a Secchi disk (Broyer *et al.* 2016), calculated as an arithmetic mean of two values measured in May and June for a breeding fishpond in each breeding season. Water transparency is an important factor affecting food availability (Robin *et al.* 2014, Arzel *et al.* 2020) and therefore affects diving ducks in fishponds (Elmberg *et al.* 1993, Musil 2006). We used *reproductive investment* computed as the number of eggs × mean egg mass as a measure of energetic expenditure into reproduction. This variable expresses the nutritional investment in clutch formation and egg incubation of a given female (Owen & Black 1990, Kear 2005).

### Breeding parameters

We used several parameters of bird reproduction that are expected to be influenced by female body condition. First, for each nest (female), the first *egg-laying date* was backdated and calculated as (see also Westerskov 1950, Weller 1956, Lack 1967): *laying date* = *actual date* – *day since start of incubation* – *number of parasitic eggs*.

Two variables for clutch size (i.e. number of eggs) of a given female had to be differentiated due to a high rate of nest parasitism (Petrželková *et al.* 2013). Thus, *total clutch size* is an explicit maximum of eggs recorded in the nest of a given female prior to hatching, and *non-parasitized clutch size* is the resulting number of eggs in the clutch after subtracting the number of eggs believed to be parasitic based on different size, coloration and development stage (Lyon 1998). We considered conspecific parasitism when the egg accretion rates were greater than one per day, and staggered incubation stages among eggs within a clutch that were

unambiguous (Dugger & Blums 2001). For each female–year measurement, *mean egg mass* (MEM) (1) was calculated as the arithmetic mean of the egg mass for non-parasitic eggs, as described in Rohwer (1988):

$$\text{MEM} = \frac{1}{n} \sum_{i=1}^n (L_i \times W_i^2 \times 0.555) \quad (1)$$

where MEM is the mean egg mass (mm<sup>3</sup>) of the (non-parasitized) clutch, *n* is the number of non-parasitic eggs, *L<sub>i</sub>* is the length (mm) of egg *i*, and *W<sub>i</sub>* is the width (mm) of egg *i*. Finally, *hatchability* indicated the proportion of the total number of eggs recorded as successfully hatched in each nest.

### Statistical analyses

Our analysis proceeded in three stages. First, we calculated a tarsus-based body condition index (BCI) of late-incubating females as these are the females that successfully produced offspring, and secondly we assessed the effect of biotic and abiotic variables on body condition. Finally, we studied the effect of body condition on the female's breeding parameters.

Previous descriptive studies in ducks have used the residuals from the regression of (log-transformed) body mass on a (log-transformed) measurement of body size as a proxy of body condition (see also Hughes *et al.* 2019, Grimaudo *et al.* 2020). A proxy based on this simple bivariate relationship is, however, severely compromised by ignoring the steady decline in body mass during egg-laying and clutch incubation (Gloutney 1989, Owen & Black 1990). Peig and Green (2009) developed another method for calculating body condition, a scaled mass index, that is widely used in other studies (English *et al.* 2018, Klimas *et al.* 2020, Parejo *et al.* 2021). However, the

scaled mass index does not allow inclusion of the incubation stage in its calculation. Therefore, we define our body condition index including the incubation stage (number of days before hatching) as an additional predictor of body mass in the regression.

The body condition of migrating birds is often attributed to variation in lipids (Pehrsson 1987, Labocha & Hayes 2012). The residuals of the regression of body mass on tarsus length most precisely predicted fat in another *Aythya* species, the Lesser Scaup *Aythya affinis* (Schamber *et al.* 2009). Moreover, the measurement of tarsus is less susceptible to measurement errors, as it is based on the featherless bone (Snow & Perrins 1998, Kear 2005). Hence, we here developed our *body condition index* (BCI) based on tarsus length while accounting for the decline in body mass during incubation. Values of BCI were obtained as the residuals from the regression of the log of mass (g) on the log of tarsus length (cm) and on the incubation stage (number of days before hatching). Formally, the estimated regression model was a linear mixed model (LMM), specified as follows:

$$\log(\text{mass}_{f,t}) = \beta_0 + \beta_1 \log(\text{tarsus length}_{f,t}) + \beta_2 (\text{incubation stage}_{f,t}) + \mu_f + \epsilon_{f,t} \quad (2)$$

where subscripts  $f$  and  $t$  distinguish females and years, respectively,  $\mu_f$  is a female-specific random error (constant across years) and  $\epsilon_{f,t}$  is the idiosyncratic random error. Female-specific random errors were included in the model to account for repeated observations of the same individuals. Model (2) was estimated via maximum likelihood, with both random errors assumed to be homoscedastic and normally distributed. A separate model was run for each species.

The value of the BCI depicts the deviation in a female's body mass from the expected value for a typical female with the same tarsus length and at the same incubation stage. Negative BCI values indicate females with a lower-than-average body condition, and positive values indicate the opposite. For instance, a BCI of  $-0.05$  indicates that the female is *c.* 5% lighter than a typical female with the same tarsus length and at the same incubation stage. In more precise terms, the BCI measures the difference between the actual versus the expected  $\log(\text{body mass})$ . The interpretation in terms of a percentage is based on the approximate

relationship  $100(\Delta \log(\text{body mass})) \approx \% \Delta \text{ body mass}$ , which works well for small magnitudes of the BCI. The exact percentage deviation can be obtained by exponentiating the BCI; in our example with  $\text{BCI} = -0.05$ , this yields  $100(\exp(-0.05) - 1) = -4.88\%$ .

In the second stage of the statistical analyses, we assessed the effect of biotic and abiotic variables on body condition in a regression setting. We considered the following predictors for our models: *winter temperature*, *water transparency* and *reproductive investment*; these predictors were standardized before the regressions (zero mean and unit variance), facilitating the comparison of effect sizes. To account for long-term trends, we also included the *year* covariate. Again, we employed LMMs with Gaussian random effects for individual females to account for the dependency between repeated measurements.

For each species, we ran regressions with all possible combinations of the covariates ( $2^5 = 32$  different model specifications), ranked all models based on the Akaike Information Criterion corrected for small sample size ( $\text{AIC}_c$ ) and calculated the model-averaged estimate coefficients based on the  $\text{AIC}_c$  weights. Additionally, we calculated the relative variable importance (RVI) of each covariate by summing the Akaike weights across all models that included the given variable (see Arnold 2010 for more details on this procedure). RVI is bounded between 0 and 1. We used 0.5 as a conservative threshold to select important explanatory (informative) covariates (Barbieri & Berger 2004).

Lastly, we studied the effect of the BCI on breeding parameters. We modelled the relationship between BCI and each of the breeding parameters of interest separately; that is, we conducted five different regression analyses, differing in the dependent variables. The only covariates included in this stage were the BCI and year. For the breeding parameters that can be treated as continuous variables (laying date, mean egg mass, hatchability), we fitted LMMs with Gaussian error distribution and individual female random effects (Zuur *et al.* 2009). For clutch size data (total clutch size and non-parasitized clutch size), we instead fitted generalized linear mixed models with Poisson distribution, reflecting the count-type nature of the dependent variables; the rest of the model structure (most notably, the random-error structure) was identical as in the LMMs.

As in the analysis of factors affecting body condition, we applied an information-theoretic approach to perform model selection based on AIC<sub>c</sub> for each dependent variable – altogether, this procedure involved 20 different regression models for each species (5 dependent variables, each with  $2^2 = 4$  model specifications). We then calculated the model-averaged coefficients and RVIs.

Multicollinearity among the covariates was assessed using variance inflation factors (VIFs); in all regressions, all VIFs were below 2.5, indicating little collinearity (Allison 1999). All regression analyses were carried out in Stata 17 (Stata-Corp 2021); the user-contributed command *miinc* (Luchman 2014) was used for the AIC<sub>c</sub>-based model-averaging and RVI calculations.

## RESULTS

### Effect of biotic and abiotic variables on female body condition

Between 2004 and 2020, 139 breeding females of Common Pochard and 251 females of Tufted Duck caught on the nest during the incubation period were included in the analyses; some females were captured in several years, for a total of 194 and 322 female–year measurements, respectively.

*Year* was the only covariate that scored an RVI > 0.5 (Table 2) and was deemed important when explaining the variation in BCI both in Common Pochard and Tufted Duck (Fig 1). After accounting for the biases that body size (tarsus length) and incubation stage can introduce in assessments of body condition, the model-averaged regression coefficient estimate (Table 3) shows a change in body mass of *c.* 1.5% and 0.9% for Common Pochard and Tufted Duck, respectively, over the 17-year study period. For the Tufted Duck, however, the evidence for this effect is only moderate, as the  $\Delta$ AIC<sub>c</sub> from the baseline (constant-only) model was 0.36 (Table 5) and the RVI value was marginally larger than the threshold ( $RVI_{year} = 0.58$ ; Table 2).

### Effect of body condition on breeding parameters

In both species, the BCI of incubating females affected *mean egg mass* and *hatchability*; both variables were included in the best models according to the AIC<sub>c</sub> (Tables 4 and 5) and their RVIs

ranged from 0.532 to 0.994 (Table 2). Females with higher values of BCI laid larger eggs (Common Pochard:  $\beta_{body\ condition} = 9.60$ ; Tufted Duck:  $\beta_{body\ condition} = 14.24$ ; Fig 2) and a higher proportion of them successfully hatched (*hatchability*: Common Pochard:  $\beta_{body\ condition} = 2.425$ ; Tufted Duck:  $\beta_{body\ condition} = 0.428$ ). Both species also exhibited a long-term decrease in *hatchability* (with body condition accounted for) over the study period; this was larger in Tufted Duck (in terms of both RVI and effect size, see Tables 2 and 3).

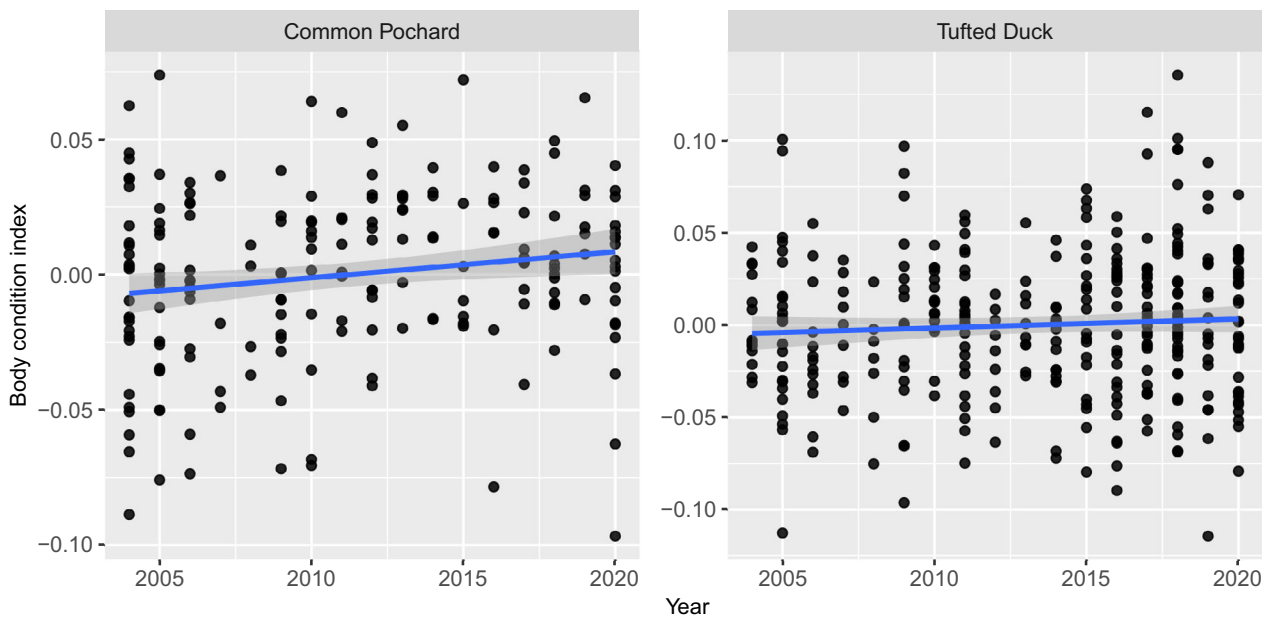
In Common Pochard, over the 17-year study period, we found a substantial long-term delay in *laying date* ( $RVI_{time\ trend} = 0.76$ ); i.e. the laying date is delayed by 4.25 days over the study period. In Tufted Duck, on the other hand, we found a long-term increase in *total clutch size* ( $RVI_{time\ trend} = 0.80$ ).

## DISCUSSION

The long-term changes in BCI of females in the late stage of incubation and the consequent effect on breeding success are crucial for an assessment of population dynamics (Johnson *et al.* 1992, Newton 2013), especially for globally declining species such as Common Pochard and Tufted Duck (Musil & Fuchs 1994, Musil & Neužilová 2009, Fox *et al.* 2016, Elmberg *et al.* 2020, Folliot *et al.* 2020, Keller *et al.* 2020, IUCN 2022). Based on the analysis of body condition in late-incubating females, our study shows evidence of improvement in the body condition both in Common Pochard and in Tufted Duck over 17 years. Moreover, we show the importance of body condition as a key predictor of mean egg mass and hatchability in these declining species.

### Long-term improvement in body condition of breeding females

The improvement in BCI at late incubation of Common Pochard and Tufted Duck females over a period of 17 years was not directly related to preceding winter conditions (indicated by *winter temperature*) affecting birds prior to the breeding season, or to the relative feeding conditions (indicated by *water transparency*) affecting birds on arrival. We found a long-term improvement in body condition both in Common Pochard and in Tufted Duck, which can be an important driver of



**Figure 1.** Effect of year on body condition index (the residuals from the regression of the log of mass (g) on (1) the log of tarsus length (cm) and (2) the incubation stage; 95% confidence interval in Common Pochard and Tufted Duck (body condition index values of individual females expressed in black circle).

**Table 2.** Regression results – relative variable importance.

Species	Independent variable	Body condition index	Dependent variable				
			Laying date	Total clutch size	Non-parasitized clutch size	Mean egg mass	Hatchability
Common Pochard	Year	0.782	0.760	0.379	0.334	0.359	0.562
	Body condition index		0.521	0.273	0.268	0.610	0.945
	Winter temperature	0.459					
	Water transparency	0.272					
	Reproductive investment	0.264					
Tufted Duck	Year	0.582	0.324	0.797	0.496	0.421	1.000
	Body condition index		0.353	0.278	0.290	0.994	0.532
	Winter temperature	0.442					
	Water transparency	0.273					
	Reproductive investment	0.341					

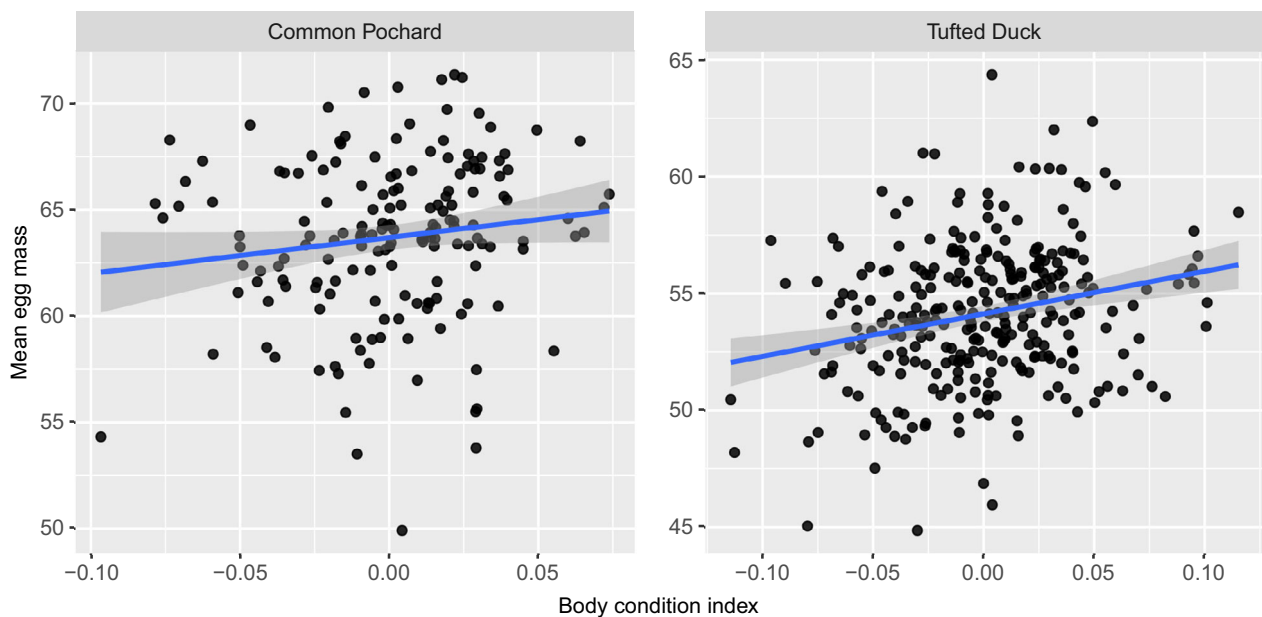
change in the population dynamics of these species (Blums *et al.* 2005, Guillemain *et al.* 2010, Newton 2013, English *et al.* 2018) as females in better body condition are expected to be more capable of incubating clutches and raising offspring.

Regardless of the benefits of improved body conditions for the population dynamics of the species, both species have been declining alarmingly in recent decades (Keller *et al.* 2020). Contrary to previous studies showing a clear association



**Table 3.** Regression results – model-averaged coefficient estimates.

Species	Independent variable	Body condition index (linear)	Dependent variable				
			Laying date (linear)	Total clutch size (Poisson)	Non-parasitized clutch size (Poisson)	Mean egg mass (linear)	Hatchability (linear)
Common Pochard	Year	0.000903	0.245	0.00181	0.00129	-0.0203	-0.00510
	Body condition		-0.0436	-0.0629	-0.0436	9.603	2.425
	Winter temperature	-0.00181					
	Water transparency	-0.000252					
	Reproductive investment	0.000150					
Tufted Duck	Year	0.000522	-0.0374	0.00690	0.00268	0.0181	-0.0244
	Body condition		-5.825	-0.0473	-0.0657	14.24	0.428
	Winter temperature	-0.00147					
	Water transparency	-0.000206					
	Reproductive investment	0.000735					

**Figure 2.** Effect of body condition index (the residuals from the regression of the log of mass (g) on (1) the log of tarsus length (cm) and (2) the incubation stage; 95% CI) on mean egg mass in Common Pochard and Tufted Duck (body condition index values of individual females expressed in black circle).

between female body condition and widespread declines in a North American *Aythya* species (Lesser Scaup *Aythya affinis*; Anteau &

Afton 2004), our results show that population declines cannot be directly linked to changes in body condition, as we found an increasing trend in

**Table 4.** Results of the model selection procedure for Common Pochard.

Dependent variable	Rank	Model	AICc	$\Delta_i$	$w_i$	ER
Body condition index	1	Year + winter temperature	674.86	0	0.217	1
	2	Year	674.98	0.127	0.204	1.07
	3	–	676.76	1.902	0.084	2.59
Laying date	1	Year	-1480.52	0	0.384	1
	2	Body condition index	-1478.58	1.936	0.146	2.63
	3	–	-1477.72	2.803	0.095	4.06
Mean egg mass	1	Body condition index	-915.07	0	0.378	1
	2	–	-914.35	0.720	0.264	1.43
Hatchability	1	Year + body condition index	-209.28	0.000	0.539	1
	2	Body condition index	-208.71	0.567	0.406	1.33
	3	–	-203.65	5.632	0.032	16.71
Total clutch size	1	–	-1012.63	0	0.488	1
Non-parasitized clutch size	1	–	-990.93	0	0.454	1

Notes: (1) AICc = Akaike information criterion with small-sample correction.  $\Delta_i$  = AICc difference between the top model (model ranked first) and model  $i$ ;  $w_i = \exp(-\Delta_i/2)$  = Akaike weight of model  $i$ ; ER =  $w_i/w_1$ , the evidence ratio for model  $i$ . (2) Following Arnold (2010), we discarded models with *uninformative parameters*, i.e. models whose AICc can be improved by dropping some of the covariates.

**Table 5.** Results of the model selection procedure for Tufted Duck.

Dependent variable	Rank	Model	AICc	$\Delta_i$	$w_i$	ER
Body condition index	1	Year + winter temperature	1055.78	0	0.161	1
	2	–	1056.13	0.358	0.135	1.2
Laying date	1	–	-2585.55	0	0.435	1
Mean egg mass	1	Body condition index	-1452.58	0	0.577	1
	2	Year	-1442.04	10.533	0.003	193.74
	3	–	-1441.96	10.620	0.003	202.35
Hatchability	1	Year + body condition index	-291.65	0	0.532	1
	2	Year	-291.40	0.254	0.468	1.14
	3	–	-261.67	29.978	0.000	3233595.87
Total clutch size	1	Year	-1728.95	0	0.443	1
	2	–	-1726.23	2.720	0.114	3.896
Non-parasitized clutch size	1	–	-1690.56	0	0.359	1

Notes: (1) AICc = Akaike information criterion with small-sample correction.  $\Delta_i$  = AICc difference between the top model (model ranked first) and model  $i$ ;  $w_i = \exp(-\Delta_i/2)$  = Akaike weight of model  $i$ ; ER =  $w_i/w_1$ , the evidence ratio for model  $i$ . (2) Following Arnold (2010), we discarded models with *uninformative parameters*, i.e. models whose AICc can be improved by dropping some of the covariates.

BCI. Folliot *et al.* (2020) failed to confirm changes in adult survival as the main explanatory variable of a decline in Common Pochard populations. A lower proportion of breeding females within populations – resulting in higher male bias in the adult sex ratio (Brides *et al.* 2017, Frew *et al.* 2018, Pöysä *et al.* 2019) – has been observed in many duck species. A lower proportion of females is critical for population change and can lead to rapid decline of reproductive success when fewer females reproduce. Moreover, the knowledge of

what proportion of females breed in a given year is very limited (Poláková *et al.* 2018, P. Musil unpubl. data). It is possible that in poor years only females with high BCI are able to breed successfully (e.g. Uttley *et al.* 1989). As we analysed only females that successfully incubated clutches up to the late stage of incubation, this could have increasingly biased our data towards females in better condition if environmental conditions declined over time. Furthermore, studies focusing on survival in earlier life stages among *Aythya*

species, i.e. offspring survival to fledging (Dawson & Clark 1996, Blums *et al.* 2002, Broyer 2019) and post-fledging survival to recruitment to the breeding population (Messmer *et al.* 2021), are lacking in the literature. Both of these demographic variables alongside a lower proportion of females breeding could cause a population decline and are important issues for future studies on population dynamics of these species.

Under ongoing climate warming (Hurrell & Deser 2010), we expected that the increasing winter temperatures could positively affect the body condition of diving ducks. However, we found no direct effect of winter temperature on the body condition in these species. The higher values of body condition of breeding females may be related to the environmental variability of winter/early spring weather conditions throughout their wintering distribution in Europe (Guillemain *et al.* 2013), shifts in spring phenology on breeding grounds (Podhrázký *et al.* 2017) and long-term changes in habitat use in the wintering grounds (Musilová *et al.* 2021). These changes in habitats and spring phenology could influence female body condition through indirect effects (Sedinger & Alisauskas 2014). A long-term improvement in the body condition of breeding females in the temperate zone may be linked to a higher availability and suitability of wintering habitats close to the breeding grounds, reduced energetic costs and more feeding opportunities during winter minimizing winter carry-over effects (see Inger *et al.* 2010) or an increase in their survival (Haramis *et al.* 1986, Devries *et al.* 2008, Guillemain *et al.* 2008, Newton 2013, Podhrázký *et al.* 2017).

Another possible explanation of the improved body condition indirectly driven by climate change could be found in the recent shortening of the migration distance between nesting and wintering grounds, as was recently evidenced for Greylag Goose *Anser anser* (Podhrázký *et al.* 2017) and Bewick's Swan *Cygnus columbianus bewickii* (Nuijten *et al.* 2020). The shortening of migration distance can be further demonstrated in Tufted Duck and other waterbirds as a shift in their wintering distribution (Lehikoinen *et al.* 2013, Pavón-Jordán *et al.* 2019). The body condition of breeding females may arise from a shortening of migration distance due to the lower energy cost of regulating body heat to survive the winter and thus only

slight body condition loss during the time spent at stopovers and on wintering grounds (Piersma 2002, Newton 2007). From a long-term effect perspective, all these effects could plausibly influence the body condition of long-lived migratory capital breeders such as Common Pochard and Tufted Duck.

### Breeding parameters are driven by female body condition

Our study provides evidence that females in better body condition laid larger eggs in both studied species, consistent with the results of nest studies on diving ducks where a high value of body condition were found to be important during clutch incubation and linked to a larger clutch size (Blums *et al.* 2005, Warren *et al.* 2013, Folliot *et al.* 2017). It is worth noting that good female body condition is in general important during egg-laying among birds (Ryder 1970, Owen & Black 1990, Kear 2005).

Egg mass is considered a good predictor of future duckling growth and survival (Dawson & Clark 1996, Pelayo & Clark 2002). Larger eggs contain a greater amount of essential nutrients (Ricklefs *et al.* 1978) and hatched offspring are then predicted to be heavier, structurally larger (Grant 1991, Reed 1999, Hořák *et al.* 2007) and have higher survival (Lepage *et al.* 2000, Blums *et al.* 2002), which is critical for population productivity. By contrast, Alisauskas and Ankney (1992) suggested that females in better body condition are expected to produce more eggs, which opens the debate about the widely studied trade-off between egg mass and clutch size (Rohwer 1988, Blackburn 1991, Figuerola & Green 2006). Consistent with our results, both Common Pochard and Tufted Duck females with higher values of body condition use the strategy of nutrition investment in larger egg mass rather than in a larger number of eggs in the clutch. Similarly, Hořák *et al.* (2008) failed to find any correlation between egg mass and clutch size in Common Pochard probably because they did not consider female body condition as an important factor for clutch formation (Alisauskas & Ankney 1992, Kear 2005).

Importantly, females in better body condition showed higher hatchability, which is probably linked to the higher nutritional reserves positively affecting incubation behaviour (Arnold

*et al.* 1995). Females in good body conditions probably minimize their time spent off the nest during clutch incubation and thus minimize the probability of clutch predation and increase their hatchability. It is important to note that the females included in the hatchability analysis represent a subset of the local breeding population that incubated clutches long enough to be captured in the late stage of the incubation period, and the nest survived to this stage. We also consider that the methodological approach was consistent during the whole study period and cannot be considered a source of bias in data analysis.

Our results also revealed a delay in laying date of Common Pochard over the study period, which is not related to changes in female body condition but to some other factor acting over time that we have not measured. Similarly, the long-term increase in total clutch size (including parasitic eggs) in Tufted Ducks was not directly associated with the long-term improvement in female body condition. Such an increase in clutch size may be linked to an increased frequency of nest parasitism (Neužilová & Musil 2010, Štátný & Hudec 2016, Čehovská *et al.* 2019). Moreover, the rate of nest parasitism increases later in the breeding season, which could lead to larger clutches of Tufted Duck observed at the time of female trapping (Neužilová & Musil 2010). Moreover, increased clutch size may cause nest abandonment (Blums *et al.* 1997, Kear 2005), leading to a decrease in hatchability, as shown in this study.

The decline in hatchability, which we found was not linked to female body condition, the delay in laying date of Common Pochard and the increase in clutch size in Tufted Duck (see also Dugger & Blums 2001) suggest that although females are currently in better body condition compared with two decades ago, there are other factors that are the major drivers of population declines. Deteriorating conditions in the main breeding habitat (e.g. Pavón-Jordán *et al.* 2017, Santangeli & Lehikoinen 2017), such as lower water transparency (Blindow *et al.* 1993, Moss *et al.* 2004) and lower food availability, increased heat stress (Ma *et al.* 2014), and inter- and intra-specific competition for space and resources (Bethke 1991, Elmberg *et al.* 1997, Pöysä & Pöysä 2002), probably prevent Common Pochard and Tufted Duck from improving their overall breeding success and from helping to revert their population declines in Europe.

## CONCLUSION

Our results did not provide any evidence of a reduction in body condition of female Common Pochard and Tufted Duck at the late incubation stage over last two decades (2004–2020). Even though we did not reveal any biotic or abiotic variable acting prior to and at the time of nesting that could explain annual variation in female body condition, the decreasing population size of Common Pochard, as well as Tufted Duck, could be related to changes in population structure (proportion of breeding females and/or in duckling survival) closely connected to limited food availability in the later part of their breeding seasons.

Over the 17 years of study, we found that females breeding in Czechia do not suffer from reduced body condition, and body condition is positively related to their breeding output (females in better body condition produce larger eggs and have a higher hatchability). Nevertheless, overall hatchability is decreasing, which should be accounted for in future population studies. Moreover, we note the necessity of a future focus on post-hatching periods such as juvenile recruitment and survival, rather than adult survival, especially in the case of the declining populations of Common Pochard and Tufted Duck in Europe (Keller *et al.* 2020).

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## AUTHOR CONTRIBUTIONS

**Dorota Gajdošová:** Formal analysis; methodology; resources; supervision; visualization; writing – original draft; writing – review and editing. **Petr Musil:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Jan Zouhar:**

Conceptualization; data curation; formal analysis; investigation; software; writing – original draft; writing – review and editing. **Zuzana Musilová:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Sárka Neužilová:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Diego Pavón-Jordán:** Data curation; formal analysis; writing – review and editing.

## CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

## ETHICAL NOTE

None.

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## Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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