Seasonality, diet, and physiology as a predominant control factors of the moult dynamics in birds – a meta-analysis

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Abstract

Moult is a process, usually occurring annually, in which birds replace their plumage. It is one of the most crucial life-history traits because it restores the functions of plumage and allows a bird to adapt to environmental conditions or special seasonal needs such as breeding and camouflage during non-breeding season. Consequently, moulting has advantages in terms of future performance. However, it also has immediate costs related to producing protein-rich tissue, reduced thermoregulation and flight performance. Expression of such costs may depend on a wide array of physiological and environmental factors experienced by an individual. Considering a variety of factors affecting moult dynamics in single studies, we use a systematic meta-analytical approach to summarise existing evidence and look for general patterns in how moult depends on both extrinsic (environment, ecological variability) and intrinsic (physiology, energy reserves, life stage) factors.

Our analysis has indicated that patterns of moult dependency on the studied moderators are multifaceted and non-uniform across different ways of measuring moulting. The moult process seems to be conservative and tightly scheduled within an annual lifecycle of an individual, but some of its components may be more flexible and provide necessary plasticity in response to specific factors. Within the conservative framework of moult onset, duration, completion and strategy, moult intensity and score may be further modified by environment and energy reserves (diet, breeding time and breeding success). Moreover, the species-specific reliance on specific cues had likely evolved in close link to their environments. Taxa moulting in a cold/temperate climate are the most susceptible to seasonal changes, in contrast to birds which moult in (sub)tropics. The latter are influenced the most by diet and physiology. Altered seasonality observed in cold and temperate regions may disrupt phenological matches that had been fine-tuned over long evolutionary history. For birds, which have a complex annual cycle and plenty of tightly scheduled energy-demanding activities (migration, breeding, moulting), even small changes may impose fitness costs.

In the meta-analysis, we detected temporal changes in effect sizes revealed by a negative correlation between effect sizes and year of publication. The reason that early studies detected bigger effect sizes may be explained by methodological quality of small trials. An alternative explanation of the observed pattern may suggest changes in phenological process involving more independent physiology from external conditions which could turn out into unreliable predictors of future conditions in time of rapid global changes.

Key words: birds, moult dynamics, moult parameters, feathers replacement, adaptation, experimental studies, observational studies, seasonal variation, global warming, meta-analysis

Contents

I. INTRODUCTION

Feathers perform a number of functions for a bird: they play an important role in thermoregulation (Wolf & Walsberg, 2000), water repellence (Rijke, 1970), flight (Williams & Swaddle, 2003) and in camouflage (Beltran, Burns, & Breed, 2018). Their colours and patterns are used to send signals to attract mates and scare off rivals (Peters, Kingma, & Delhey, 2013). They are regularly maintained by a variety of behaviours, but through wear and tear as they age they are continuously degraded (Weber *et al.*, 2005). Because feathers are non-living keratinous structures, the only mechanism for damage repair is a complete replacement through the periodic process of moult. Apart from keeping the plumage in good condition, moult serves also other purposes: it allows a bird to adapt to environmental conditions or special seasonal needs such as breeding or camouflage during non-breeding season (Zimova *et al.*, 2018). Consequently, moulting has advantages in terms of future performance as it replenishes an important bodily function and adjusts it to current needs. However, it also has immediate costs. Replacing feathers requires a bird to produce large volumes of protein-rich tissue, which is both energetically and nutritionally costly (Guillemette *et al.*, 2007; Murphy & King, 2007). Moreover, periods of reduced feather numbers (i.e. in between loosing old ones and completing the growth of new ones) are usually associated with reduced flight performance or agility, exposing individuals to negative factors such as predation (Lind, Gustin, & Sorace, 2004). Expression of such costs may depend on a wide array of physiological and environmental factors experienced by an individual. Because of plumage renewal being a critically important life-history stage within the annual cycle, the internal and external bases of the control of the time and rate of moulting are of considerable interest (Bridge, 2011).

Moult dynamics can be characterized by its timing (onset, duration, termination) and intensity. It may show some flexibility in response to a bird's individual features and body condition as well as ecoclimatic and external environmental factors experienced by an individual (Dawson & Sharp, 2010; Visser *et al.*, 2011; Dominoni, Quetting, & Partecke, 2013; Machín *et al.*, 2018; Hudin *et al.*, 2018). A variety of mechanisms exist to ensure that such a demanding lifecycle event never occurs under unfavourable conditions (Flinks, Helm, & Rothery, 2008). Sets of various clues and proximate mechanisms allow a bird to fit moult within a limited time during its lifecycle (Hall & Fransson, 2000). In temperate climate long daylengths are required to initiate moult (Dawson *et al.*, 2001). Once moult has started, a decrease in photoperiod increases the rate at which moult proceeds. Such a clue allows individuals that start the moult process late still to finish moulting before unfavourable winter conditions or before the commencement of winter migration (Gwinner, Dittami, & Gwinner, 1983; Barshep *et al.*, 2013a). However, feathers grown during a more rapid moult are of poorer quality, and this presumably reduces a bird's future performance (Dawson *et al.*, 2000). If the photoperiodic cue is very weak e.g. in tropics, birds may respond to low light intensity as a predictive cue for rainfall (Gwinner & Scheuerlein, 1998). The pattern of the timing of moult coinciding with rainfall periods is, perhaps, an adaptation to carry out this energy-demanding activity during periods of food abundance (Barshep *et al.*, 2013b). Energetic cost of moult may represent up to 20% of the daily energy expenditure (Murphy & King, 2007). Thus, insufficient or low-quality diet delays the peak of moult intensity (Cristol *et al.*, 2014), reduces moult duration and adversely affects feather quality (Pap *et al.*, 2008) with potential disadvantages for flight efficiency, thermoregulation and ornamentation. Each species' moult strategy should be adapted to attain the best plumage quality within the constraints imposed by all of the aforementioned factors.

In addition to the impact of the environment itself, divergent moult strategies may vary within species in response to sex and changing states of individuals e.g. from juvenile to adult (Hemborg & Merila, 1999; Pérez-Tris *et al.*, 2001), from active breeding to failed-breeding or non-breeding (Alonso *et al.*, 2009; Bond, Konyukhov, & Jones, 2013; Crossin *et al.*, 2013). Generally, between-sex differences in several physiological, morphological, behavioural and ecological characteristics may cause differences in moult dynamics. For example sex with less investment in parental care during chick-rearing can allocate energy more readily to feather replacement (Hemborg, 1999; Neto & Gosler, 2006). Moreover, interspecific variation in breeding effort within one sex may also affect moult timing. For example, female willow warblers with larger broods begin their moult relatively later (which gives them a shorter time for moulting) than females with small broods (Bensch *et al.*, 1985). In extreme situations and deficiency of energy resources, moulting may be suspended for some time (Scheiman & Dunning, 2004). However, no species has been documented to skip an entire moult cycle, suggesting its key importance to life cycles (Humphrey & Parkes, 1959). Despite this huge variation in moult patterns and their great sensitivity to various factors, moulting is one of the most poorly studied life-history events.

Considering a variety of factors affecting moult dynamics in single studies, we decided to use a systematic meta-analytical approach to summarise existing evidence and look for general patterns in how moult depends on those factors, and which parameters in a wide array of factors experienced by birds affect moult the most. To achieve this, we have analysed the magnitudes and directions of published effect sizes quantifying moult dynamics in relation to both individual physiological characteristics, as well as environmental conditions. Recognizing factors to which moult dynamics is the most sensitive is of great importance especially now when ecosystems face an accelerating, human-induced global change linked to the process of climate warming. Also, since the collected data consists of observational and empirical results, we also explored whether the type of study has an impact on the magnitude of the effects.

In light of the abovementioned constraints and trade-offs involving moulting, we predicted it would significantly depend on both extrinsic (environment, ecological variability) and intrinsic (physiology, energy reserves, life stage) factors. In particular, in line with the published evidence, we expected that moult dynamic should vary with (i) geographical location (both between different biomes and within ranges of birds experiencing varying ecoclimatic conditions) and (ii) individual life-history correlates (e.g. migratory behaviour, age of individuals, sex). We also expected that variation will be observable between (iii) different methodological approaches to studying moult patterns, providing the first estimate of how much observed variation in moulting may reflect methodological artefacts rather than biological phenomena.

II. MATERIALS AND METHODS

(1) Literature search and study selection

We conducted a systematic literature survey in which the impact of environmental or physiological factors on moult dynamics was investigated in birds. We performed keyword searches in the *Scopus* database using combinations of the following words: moult* OR molt* AND (condition* OR environment* OR experiment* OR dependence) AND bird*. Including the two other sources of data (reference lists from extracted papers and accidentally found studies), we identified 1361 candidate studies. The last search was conducted on the 23 January 2019.

The first study was published in 1971 (Davis, 1971) and the number of published studies increased throughout the years. The highest increase of interest in moult dynamic effects was mainly during the period 1991-nowadays.

As the first step of quality control, only studies published in peer-reviewed and non-poultry science journals were included in the meta-analysis. Induced moulting in laying hens is used to recycle birds in order to enhance productivity, reduce costs and reduce industry investments in breeder farms, all of which we are not of interest in this study. Moreover, such patterns of moult would hardly reflect biological reality and would therefore likely bias our results in hard to predict ways. At the beginning, we performed filtering through the title and abstracts of each article to decide whether the article matched our selection criteria. The detailed selection process was based on the Preferring Reporting Items for Systematic Reviews and Meta-analysis (PRISMA flow diagram, Figure 1). We applied the following inclusion criteria for study selection: (i) the research was conducted on birds; (ii) the study involved experimental manipulations or field observations of moult dynamics; (iii) moult dynamics was related to environmental or physiological factors. We excluded research on the effects of date, month or year on moulting pattern when authors did not have any clear predictions for them. The reason for this exclusion is the fact that moult is an inherently temporal process, with its time dynamics. Selecting papers looking at the effect of time alone without any clear predictions would upwardly bias or effect-size estimates as in such papers the flow of time necessarily has a positive association with the moult progression metrics.

The steps for selecting and categorising data included in the meta-analysis are shown in Figure 1. Full-text articles assessed for eligibility were scanned for suitable data to calculate the Fisher's Zr statistic as a measure of an effect size. When the means, their standard deviation (SD) or standard errors (SE) were not provided in the publication, the minimum information required was a test statistic and/or *p*-value, and the study's sample size. In some articles numerical data were extracted from graphs using PlotDigitizer (http://plotdigitizer.sourceforge.net/). In case of insufficient data available for calculating an effect size, we contacted the corresponding author (15 articles) to ask them for additional information, but the response rate was low (47%). Altogether, we included 146 relevant papers, comprising 579 effect size estimates for 91 species (Table S1). A list of articles excluded during full-text filtering and reasons for exclusion are presented in Table S2.

In our meta-analysis, we focused on both the direction and magnitude of reported effect sizes. However, the direction of the outcome was not always reported, especially for a nonsignificant result. We prepared a subsample database only for records for which we were able to assess the direction of effect sizes. Rating them as negative or positive reflects the biological effects of moderator variables reported on the moult dynamics, i.e., positive signs have been assigned to longer, less intense, delayed or slower moult dynamics, whereas negative signs have been assigned to shorter, more intense, earlier or faster moult dynamics. Finally, in the subsample database we included 122 papers, comprising 414 estimates for 76 species. A larger sample of studies was used to perform the meta-analysis omitting the direction of the relationship (i.e. only looking at the strength of each moderator's impact on the moult dynamics). Below we will refer to those two subsets as Model I (subset that included directional effect sizes) and Model II (larger subset considering only directionless, absolute magnitudes of recorded effect sizes).

(2) Coding of moderator variables

For each effect size included in the analyses, the following 14 variables were extracted (see Table 1). Each general broad variable was divided in specific traits. The response and moult modulator variables were recorded as described in the original publications and then grouped into broad categories (Table 2).

(3) Statistical analyses

(a) Meta-analyses models

We employed a sequence of meta-analytic general linear mixed models to study variation and overall magnitude of published effect sizes of moult dynamics. The general form of the model is:

$$x_j \sim \mu + a_j + s_j + t_j + m_j + e_j,$$

where $\mathbf{a} \sim N(\mathbf{0}, \sigma^2(a)\mathbf{A})$; $\mathbf{s} \sim N(\mathbf{0}, \sigma^2(s)\mathbf{I})$; $\mathbf{t} \sim N(\mathbf{0}, \sigma^2(t)\mathbf{I})$; $\mathbf{m} \sim N(\mathbf{0}, \sigma^2(m)\mathbf{M})$ and $\mathbf{e} \sim N(\mathbf{0}, \sigma^2(e)\mathbf{I})$. In this model, x represents the response variable; a, s and t are additive contributions of random effects of phylogeny, species and study ID (assumed to be sampled from normal distributions with means zero and respective variances of $\sigma^2(a)$, etc.); **A** is a phylogenetic correlation matrix quantifying the degree of species dependence due to share evolutionary history; e represents a random residual and m is the study-specific effect size sampling variance (all variance form the diagonal of the **M** matrix).

In the initial model, we tested the overall effect size model which also accounted for phylogenetic dependency of meta-analytic residuals. The phylogenetic tree was obtained from a recent phylogeny of birds (Jetz *et al.*, 2012). Besides phylogenetic effect, the random terms included species and study ID. The phylogenetic random effect appeared non-significant (Model I, likelihood ratio test: χ^2= 2.99, df=1, p=0.08; Model II, likelihood ratio test: χ^2= 0.63, df=1, *P*=0.43). According to the Akaike's information criterion, the model including phylogenetic effect was not significantly better than the simpler model with a non-phylogenetically structured species random effect (Model I: $AIC_{phylo} = -14.2$; $AIC_{non\text{-}phylo} = -13.3$, $\Delta AIC < 2$; Model II: $AIC_{phylo} = -646.9$; $AIC_{non\text{-}phylo} = -648.3$, $\Delta AIC < 2$). The inclusion of a non-significant phylogenetic effect might further erode the statistical power of the model, and thus it was excluded from further analyses.

Following the above-mentioned analyses, we also tested a full model with all fixed moderators: study type, sex, age, geographical location, breeding type, developmental mode, family living, food preferences, habitat preferences, migratory status, moult modulator category, dependent variable category, data source, and random moderators: species, study ID. In the full model we considered the following interactions between moderators (representing biologically-relevant hypotheses we aimed at considering): moult modulator category*migratory status, moult modulator category*dependent variable category, moult modulator category*study type, moult modulator category*geographical location, breeding type*family living, geographical location*food preferences, moult modulator category*food preferences, geographical location*breeding type*family living. Non-significant interactions and moderators were removed, starting with the highest-order ones. All models were analysed using the ASReml-R package (Butler *et al.*, 2007)

For the above-mentioned models, we calculated heterogeneity I^2 of effect sizes as the percentage of the variance between effect sizes that cannot be attributed to sampling error nor to other random effects (Nakagawa & Santos, 2012). I^2 values around 25%, 50% and 75% are considered as small, moderate and high levels of heterogeneity, respectively (Higgins *et al.*, 2003).

As mentioned above, a large portion of published studies did not provide sufficient information to correctly assign direction to the effect size estimates. We decided to include this data in a model where all directional effect sizes were also treated as magnitudes of effect (i.e. stripped of their direction information). In order to avoid biased estimates of effect sizes, resulting from using a half-folded normal distribution (instead of the conventional normal, as in the case of directional effect sizes; (Morrissey, 2016) we took into account the fact, that the expected value of a mean of absolute normal variables is $\sqrt{\frac{2}{\pi}}\sqrt{\sigma^2(m)+\sigma^2(e)}$, in contrast to the expected mean value of a centred normal distribution, which is $\sqrt{\frac{2}{\pi}}\sigma^2(m)$. I order to account for this upward bias, we applied a transform-then-analyse (Morrissey, 2016) correction to the sampling variance of each individual effect size, $\sigma^2(m)_{xi}$:

$$\sigma^2(m)_{x_i} = x_i^2 + \sigma^2(m)_i - \left(\sqrt{\frac{2}{\pi}}\sigma(m)_i e^{-x_i^2/2\sigma^2(m)_i} + x_i\left(1 - 2\Phi\left(\frac{-x_i}{\sigma(m)_i}\right)\right)\right)^2,$$

with Φ being the standard normal cumulative distribution function.

(b) Methodological consideration

Publication bias, an important source of upwardly inflated effect-sizes in meta-analyses, was assessed using the trim-and-fill method (Duval & Tweedie, 2000). The method is based on the assumption that meta-analytical funnel plots (plots of relationships between (residual) effect size and study's sampling variance) should be symmetrical. Firstly, we created a funnel plot of meta-analysis residuals against effect sizes' measurement errors with 95% confidence intervals outlining the cone. For trim-and-fill method we used three types of estimator: L0, R0 and Q0. We also run Egger's regression test of funnel plot asymmetry using the meta-analytical residuals against effect sizes' measurement errors (Egger *et al.*, 1997).

Temporal trends in effect sizes that could indicate ‘time-lag bias’ was analysed using a simple linear model. We run a linear regression of effect size against their year of publication. All bias-control procedures were performed using *metafor* package (Viechtbauer, 2010).

III. RESULTS

(1) Model I – directions of the effect sizes

In the overall effect size model taking into account the direction of the effect sizes, our meta-analysis revealed an overall negative effect size not significantly different zero (*ES*=-0.04, 95% *CI*=-0.15 to 0.08).

In the final model, the study-type moderator explained significant differences among studies. For experimental studies, we found a stronger effect size than those observed in the wild ($F_{1,263.6} = 12.53$; $P<0.05$).

Additionally, two moderators were involved in a significant two-way interaction ($F_{36,303.1} = 1.88$; $P<0.01$). The interaction tested for the possibility that the impact of different moult modulators depended on the type of response categories. Four of the analysed moult parameters, namely moult onset, moult duration, moult completion and moult strategy were quite conservative for almost all levels of moult modulator variable. In the moult onset group, only environmental conditions negatively affected the magnitude of the effect sizes. The other moult parameters, particularly moult intensity, and moult score was more diverse in terms of effect size direction and magnitude. In the moult intensity group, diet and seasonality negatively affected the magnitude of the effect sizes, whereas breeding time had a positive effect. In the moult score group, seasonality and physiology yielded large negative effects, whereas breeding success had a positive effect. None of the parameter for moult completion group significantly differed from zero (Figure 2, Table 3).

The overall heterogeneity in the final Model I (I^2) was moderate (54%).

(2) Model II – absolute magnitudes of the effect sizes

In the overall effect size model taking into account the absolute magnitude of the effect size, our meta-analysis revealed moderate statistically significant positive effect size (*ES*=0.32, 95% *CI* = 0.23 to 0.41).

In the final model, three moderators were involved in significant two-way interactions. Firstly, the effect of moult modulators depended on geographical location ($F_{13,376.4}$ = 2.23; $P<0.01$). In the cold/temperate group, all moult modulator levels included in the final model – namely age, diet, environmental conditions, physiology and sex – showed medium effect sizes; seasonality demonstrated a considerably stronger effect size. In the sub/tropical group, diet and physiology showed the strongest effect size; environmental condition, seasonality and sex medium effect size, whereas confidence interval of age-related effect size overlapped zero. None of the moderator levels in the widespread group showed a significant effect size (Figure 3, Table 4).

Secondly, the impact of moult modulator type depended on the type of the response variable ($F_{40,428.6}$ = 1.91; $P<0.001$). Similarly to the Model I, moult onset, moult strategy and moult score showed similar moderate effect sizes with statistically significant magnitudes for almost all moult modulator levels. Only effects of diet in moult score group and seasonality in moult strategy group overlapped zero. The large and medium magnitude of the effect size of moult duration and moult intensity was significantly affected by diet, physiology, seasonality and sex, with the additional effect of diet in moult intensity group. Moult completion was mainly driven by diet, seasonality and sex and marginally not significant environmental conditions (overlapped zero only with a small fraction of their 95% *CI*; Figure 4).

The overall heterogeneity in the final Model II (I^2) was between small and moderate threshold values (37%).

(3) Methodological considerations

Visual inspection of funnel plot did not show any evidence of funnel plot asymmetry (Figure 5). The trim-and-fill method indicated no publication bias for two types of estimator used - L0 and Q0 (imputed number of missed studies was 0). Estimator R0 indicated one missing study on the right site of the funnel plot. Lack of funnel plot asymmetry was confirmed by Egger's regression tests (z=-1.08, P=0.28).

Analysis of all collected effect sizes against the year of publication provided evidence for a slightly significant temporal trend in published estimates ($F_{(1, 412)} = 4.42$; P=0.04, Figure 6).

IV. DISCUSSION

(1) Moult dynamics

Our analysis has indicated that patterns of moult dependency on the studied moderators are multifaceted and non-uniform across different ways of measuring moulting. Depending on the moult parameter considered, moderator variables have indicated an acceleration, deceleration or lack of change in the moult dynamics of birds. Four from six analysed parameters, namely moult onset, duration, completion and strategy were insensitive to bird's characteristics (age, sex) and manipulative forces (diet, environmental conditions, climate, seasonality, breeding success, breeding time, physiology and immunology). The remaining two: moult intensity and moult score were more flexible and responded strongly to external cues and bird strategy.

Moult is a highly energy-demanding activity (Lindström, Daan, & Visser, 1994); nutritional limitation, supplementation as well as quality of diet itself may modulate its dynamic. Our meta-analysis showed that moult intensity was the most sensitive to diet alterations. It is in line with individual results: a well-balanced diet (Pap *et al.*, 2008) and additional dietary flavonoids (Pap *et al.*, 2009; Cecere *et al.*, 2016) enhanced the process of feather renewal. Flavonoid-enriched food may facilitate pigment synthesis, whereas good quality food accelerates the process by providing energy required for feather keratin production, but also to compensate for altered thermoregulation and reduced foraging efficiency (Murphy, 1996).

Because of high energy demand, moult is separated in time from other costly events, like reproduction or migration (Echeverry-Galvis & Hau, 2012). Such separation maximizes outcomes of both processes. Nevertheless, some species are able to overlap moult and breeding/migration. Most often, such co-occurrence is observed only for a few days. In extreme cases e.g. some tropical bird species, full overlap of breeding and moulting exist. Consequences of such overlapping manifested in slower and less intense moult rates as demonstrated in our meta-analysis. It is likely that this kind of strategy is promoted in environments with little seasonal variation and high food abundance (Foster, 1974), whereas it is absent in species that experience highly seasonal variation.

In mid- and high-latitude species moult is usually temporally constrained between the end of reproduction and the onset of migration or wintering (Holmgren & Hedenström, 1995). In our meta-analysis, photoperiod (the annual change in day length) was one of the major seasonality-linked factors included in the analysis, and it significantly direction of moult intensity and moult score and magnitude of moult components except moult strategy. In laboratory condition, when the day length becomes rapidly shortened (decreasing photoperiod), moult speed accelerated in individuals exposed to such conditions (Griggio *et al.*, 2009). The analogous effect was visible in moult score which describes the state to which moult has advanced at the time when a bird was examined. Seasonality change, expressed as a photoperiod shift from short-days to long-days, caused an increase in moult scores (Pereyra, Sharbaugh, & Hahn, 2005; Flahr *et al.*, 2015). The initial predictive cue – seasonality – may be supplemented with additional external signs e.g. snow cover (Marmillot *et al.*, 2016), temperature

(Barshep *et al.*, 2013a) and rainfall pattern (Barshep *et al.*, 2013b). It allows fine-tuning of moult timing to local, and year-specific, conditions. Reliance on a wide range of environmental cues allow birds to strategically manage time and energy in a way that is thought to fit moult within limited time and maximize their fitness. In order to maximize fitness bird can allocate their limited resources into self-maintenance (a new set of feathers) or current reproduction. In the meta-analysis we observe a competition between feather replacement and breeding for limited time, nutrients and/or energy. Parental investment influenced the moult dynamics leading to differences in moult scores (Figure 2). Successfully breeding birds replace less feathers than non-breeders or failed breeders (Alonso *et al.*, 2009; Crossin *et al.*, 2013). Moreover, individuals that overlapped breeding and moult tended to moult fewer feathers simultaneously and exhibited longer intervals between shedding consecutive feathers (Figure 2). Additionally, moult score was modulated by physiological state of organism not connected to breeding effort e.g. condition of the bird (Barron, Webster, & Schwabl, 2013) including endogenous rhythms (Pant & Chandola-Saklani, 1993, 1995). This association suggested that immunological challenge may also play an important role in moult dynamics. However, we did not find any positive or negative effect across all studied moult characteristics. It may, however, reflect the fact, that in our meta-analysis only 24 effect sizes represented this particular type of condition dependence.

Based on sex-specific physiology and behaviour, we can predict that females moult later than males because, in general, females have higher nesting and post-fledging parental investment than males (Hemborg & Merila, 1999). Similarly, we can predict that juveniles, stressed by time and limited by their overall worse physiological condition and foraging competency moult less feathers than adults (Marchetti & Price, 1989; Wunderle, 1991). Both relations described above were not detected in our meta-analysis. Some studies included in this meta-analysis attempted to examine sex- and age-specific effects of moult characteristics but the availability of such specific results is surprisingly low. We collected only 43 effect sizes concerning age-specific effects and 109 sex-specific effect. Clearly, considerable proportion of this data loss is due to not reporting non-significant age/sex effects. We recommend that future studies documenting moult dynamics report inter-individual variation in phenology with respect to sex or age even if they are not significantly different.

In conclusion, the moult process seems to be conservative and tightly scheduled within an annual life-cycle of an individual, but some of its components may be more flexible and provide necessary plasticity in response to external factors. Within the conservative framework of several moult parameters, such as onset, duration, completion and strategy, moult intensity and score may be further modified by environment and energy reserves. Flexibility of these specific measures is likely due to greater ease of modifying intensities of physiological processes rather than its biological timing. In other words, seasonal activities must be accurately timed because mismatches with the environment can have severe fitness consequences. Because of this, timing of lifecycle processes is also likely to be under stronger genetic control than their resource-related intensity.

(2) Type of study: experiments versus observational studies

To understand ecological and evolutionary processes we can use different methods: design an experiment and/or perform observations in the natural world. Our meta-analysis considered data coming from 64 experimental studies (238 effect sizes) and 83 observational studies (341 effect sizes). The latter gave significantly weaker effect sizes than experiments. Interpretation of this difference is easiest assuming, that experiments control many confounding factors and therefore are able to deliver more precise effect size estimates, stripped of the impact of unexplained biological noise. However, the difference observed in our analysis should not prejudge on the quality of the result because each method has its own advantages and limitations.

Some of the observational studies do not have their experimental analogues and vice versa – some of the experimental studies do not have equivalent observations in natural conditions. In our meta-analysis, all effect sizes studying climatic variables are exclusively observational. Profound environmental crisis we face today e.g. in the form global climate change are all very difficult to study by manipulating variables and repeating experiments (Sagarin & Pauchard, 2012). The scale and the dynamics of climate have leapt beyond the scales of time and space that are readily controlled in experiments. Similarly, from the literature survey, we extracted more than three times more effect sizes investigating the effect of environmental conditions in nature than during experimental manipulations. Simply, such systems are too large and complex for ecologists to manipulate (Macnab, 1983). In turn, manipulation of diet quality and food availability, immune response and light conditions are the domain of experimental research.

(3) Different factors shape moult dynamics in different geographical locations

Birds are arguably the most ubiquitously distributed vertebrate taxon throughout the globe (Claramunt & Cracraft, 2015). They occupy a huge variety of habitats and are found in the tropics as well as at the extremes of latitude and elevation gradients. The cyclical replacement of feathers is the process which facilitates the global success of birds. After all, it is the feathers that allowed birds to persist in such diverse environments providing them with the ability to fly and with unique thermoregulatory capabilities. However, in a periodically changing environment, it is important for animals to properly time the major events of their life in order to maximise their lifetime fitness (Barta *et al.*, 2006).

Birds typically use a combination of physiological mechanisms and environmental cues to ensure that such energy-demanding processes like breeding, moulting and migration occur without major temporal overlap and under the most favourable conditions (Flinks *et al.*, 2008). Significant interactions in our meta-analysis, involving geographical range of each species, clearly indicate that birds from different regions use divergent cues to time and execute the moulting process. Taxa moulting in a cold/temperate climate are the most susceptible to seasonal changes, in contrast to birds which moult in (sub)tropics. The latter are influenced the most by diet and physiology. For widespread taxa which occur around the world, we did not find any clear factor affecting moult dynamics. It is important to note that in our analysis this group included only five species, in comparison to cold/temperate birds which included 67 species, and (sub)tropical birds counting 19 species in the analysed dataset.

The species-specific reliance on specific cues had likely evolved in close link to their environments. Photoperiod (included as a predominant factor in the seasonality category) appears to be the critical driver of moult in cold and temperate regions (Beltran *et al.*, 2018). The adaptive significance of responding to photoperiod is that daylength is a reliable predictor of average future conditions e.g. the upcoming winter. At the same time, these species seem to remain generally unresponsive to other temporary changes in the environment because other features vary irregularly and are poorer predictors of the future (Payne, 1972). Naturally, other factors for instance temperature and nutrition can modulate moult timing, but only if photoperiod - initial predictive cue appears (Beltran *et al.*, 2018).

In contrast, tropical residents and species that are subject to consistent annual daylength may rely heavily on non-photoperiodic cues e.g. food abundance. Furthermore, wild tropical birds, not constrained by migration or harsh winter weather, might have greater opportunity to replace feathers more slowly than temperate birds (Freed & Cann, 2012). They may interrupt moult to breed and are thought to be more likely to stop or start moulting if resources' availability changes (Class & Moore, 2013). Because in tropics there is no a single favourable seasonal window, any environmental disturbance that reduces food availability during the moulting season can slow down or even stop feather replacement in order to reduce daily energy expenditures (Freed & Cann, 2012). Contrary, birds with supplemental food effectively increased their ability to carry out an expensive life-history stage (Class & Moore, 2013). Food availability is strictly connected with physiology of organisms, which is clearly visible in our results. Physiology is the second factor affecting moult dynamics with the highest magnitude of effect size (Figure 3). Taking into account energetic cost of moult ranging from 10% increase in metabolic rate in red knots *Calidris canutus* (Vézina, Dekinga, & Piersma, 2010) even to 82% in white-plumed honeyeaters *Lichenostomus penicillatus* (Lindström, Visser, & Daan, 1993) an individual has to be in good condition to bear such a big additional energetic burden.

(4) Phenological (mis)matches in a changing world

Currently observed rapid global changes, especially global warming, may disrupt phenological matches that had been fine-tuned over long evolutionary history. One of the first evident effects is the alterations in phenology or timing of annual events across different animal and plant taxa (Tomotani *et al.*, 2018; Kiat, Vortman, & Sapir, 2019). For birds, which have a complex annual cycle and several tightly scheduled energy-demanding activities (breeding, moulting, migration), even small changes may impose fitness costs.

The fastest changes related to warming are observed in cold and temperate regions. Altered seasonality is visible in advanced or extended growing season, or by uneven warming patterns across the year. Our meta-analysis showed that seasonality was a key factor modulating moult dynamics in these areas. Changes in annual routine begin to be observed in natural populations. Long term study conducted in the Netherlands on a population of European pied flycatchers (*Ficedula hypoleuca*) showed different rate of advancements in the timing of phenological processes. Timing of moult advanced faster than spring migration and breeding. Even though the authors did not detect a correlation with the temperature to explain the shift, these changes may be caused by shifts in photoperiod experienced by birds at birth, which in turn may result from climate-change driven alteration of life-history (Tomotani *et al.*, 2018). Another long-term study conducted on a passerine bird species that breed in the Western Palearctic ecozone showed a significant correlation between increased extent of the post-juvenile moult and global warming over the last 200 years (Kiat *et al.*, 2019).

In addition to individual fitness cost caused by shifting in phenological processes, climate change may also disrupt the interaction between species, as well as interactions of individuals within a species. Recent evidence suggests that response of males and females in moult timing differ (Tomotani *et al.*, 2018). Faster moulting in males may result in a shortening of the total time available for breeding through accelerated gonadal regression (Dawson, 2006; Visser *et al.*, 2011). The mismatch has been also noticed between adults and their offspring. Synchronization between fledging of young and end of wing moult in barnacle geese *Branta leucopsis* decreased in the temperate populations (Van den Jeugd *et al.*, 2009). Furthermore, seasonal processes of organisms at different trophic levels are modified at different rates. It may lead to mismatches in life-history events timing between species that are dependent on each other (Visser & Holleman, 2001). Based on the available knowledge and trends, none of the phenological processes should be considered separately.

Biological systems require a holistic approach, especially in time of rapid global changes. Our meta-analysis revealed that beyond physiological factors, diet (including food abundance and quality) and seasonality are critical drivers of moulting. If these cues turn out to be unreliable factors of upcoming environmental conditions, it may disrupt not only one phenological process for which they are a cue but whole annual activities.

(5) Effect sizes across timeline

When time-lag bias operates, the first published studies show systematically greater effect sizes compared to subsequently published investigations (Trikalinos & Ioannidis, 2005). In the meta-analysis we detected evidence for such temporal changes in effect sizes because the correlation between effect sizes and year of publication decreased over time and approached zero in recent years. The reason that early studies are prone to overestimation of the magnitudes of the effect sizes may be smaller sample sizes than those seen nowadays (Fanelli, Costas, & Ioannidis, 2017). Moreover, it has often been suggested that such small-study effects can result also from a combination of lower methodological quality of small trials or publication bias (small studies with negative effects are unpublished or less accessible than larger studies) (Greco *et al.*, 2013). An alternative explanation of the observed pattern may suggest changes in phenological process. Smaller effect sizes over time may indicate that along with rapid climate change, birds' physiology becomes less and less dependent on external conditions, which gradually become unreliable predictors of future conditions. Time-lag bias is common in literature and has been detected in other ecological studies (Jennions & Moller, 2002) including meta-analyses (Santos, Scheck, & Nakagawa, 2011)(Sánchez-Tójar *et al.*, 2018). Detecting it in our study clearly indicates, that moult and related processes are still actively studied and constitute a developing, everchanging field of avian biology and evolutionary ecology in general.

V. CONCLUSIONS

1. Our meta-analysis, that took into account intrinsic and extrinsic factors potentially affecting moult dynamics, revealed an average negative effect size of studied factors not significantly different from zero (when taking into account effect size directions) and moderate statistically significant positive effect size (when taking into account absolute magnitudes of effect sizes).
2. Statistically significant interaction between moult modulator categories and response variable categories indicated that some moult parameters are conservative (moult onset, duration, completion and strategy), whereas others (moult intensity and moult score) are susceptible to factors like diet, seasonality, breeding time, breeding success and physiology. The annual cycle of phenological processes must be accurately timed because mismatches with the environment can have severe fitness consequences. However, intensity of life-cycle events is

much easier to modify because it depends on physiological condition and resources availability at a given moment.

3. Different factors shape moult dynamics in taxa inhabiting different geographical locations. Specifically, bird moulting in cold/temperate climate are the most susceptible to abiotic stressors, namely seasonal changes, whereas diet and physiology are more important in sub/tropics. Given the predicted climate warming over the next decades, these patterns may cause cumulative phenological changes in moult patterns and also within other annual routine events associated with moulting, especially breeding and migration.
4. Our meta-analysis included two types of studies, namely observational and experimental research. Experimental studies were characterised by on average larger effect sizes than those observed in the wild. Research investigating the effect of diet, immunology and light condition prevailed in the former, whereas focus on climate and environmental conditions was typical for the latter. Our results emphasize once again that studies should be aware of their values and constrains and draw conclusions eligible for the selected method.
5. Beyond the knowledge revealed in our meta-analysis, we also need a deeper understanding of the mechanisms controlling the organization and flexibility of the moult dynamics. This information could then be used for making predictions of how annual routine cycles will respond to environmental change.

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VIII. SUPPORTING INFORMATION

Table S1. List of studies used in the meta-analyses investigating the effect of intrinsic and extrinsic factors affecting moult dynamics

Table S2. List of articles excluded on the basis of full-text analysis

Table S3. Excel file containing the dataset (available with the journal's publication date)

FIGURES

Figure 1. PRISMA flow diagram of our data search and collection.

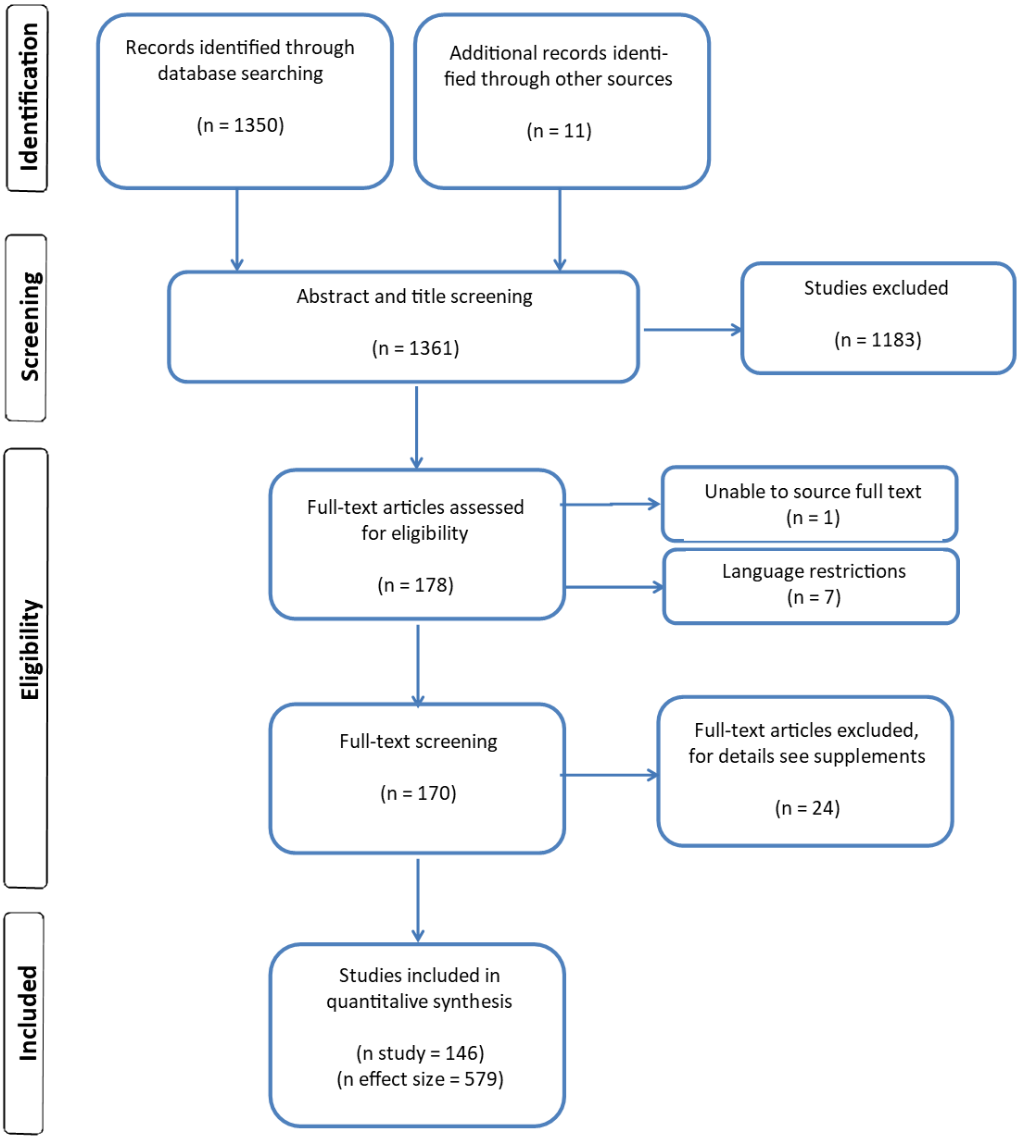


Figure 2. Results of meta-analysis showing interaction of moult modulator categories and response variable categories for Model I. Effect sizes are shown as squares with 95% confidence intervals; the overall effect size is shown by the diamond.

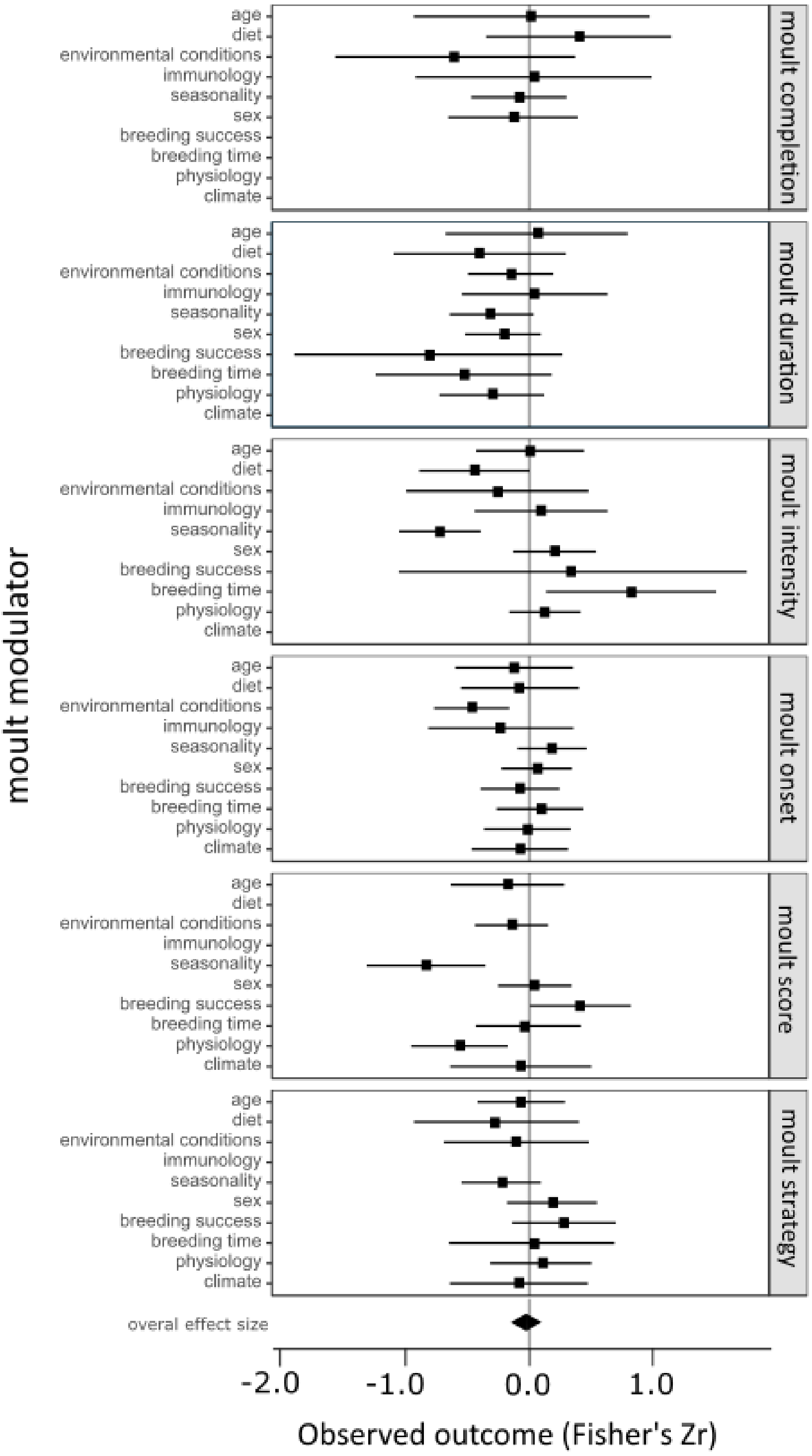


Figure 3. Results of meta-analysis showing interaction of moult modulator categories and geographical location for Model II. Effect sizes are shown as squares with 95% confidence intervals; the overall effect size is shown by the diamond.

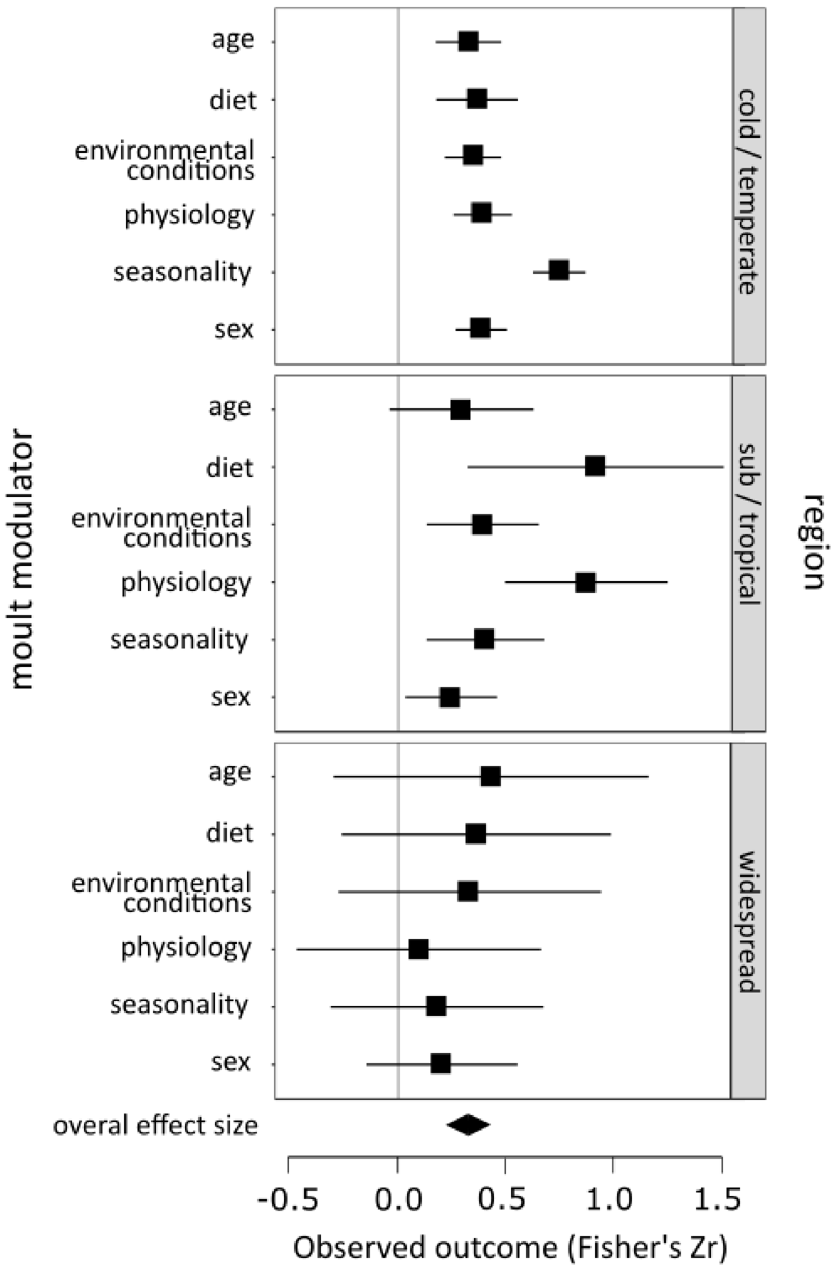


Figure 4. Results of meta-analysis showing interaction of moult modulator categories and response variable categories for Model II. Effect sizes are shown as squares with 95% confidence intervals; the overall effect size is shown by the diamond.

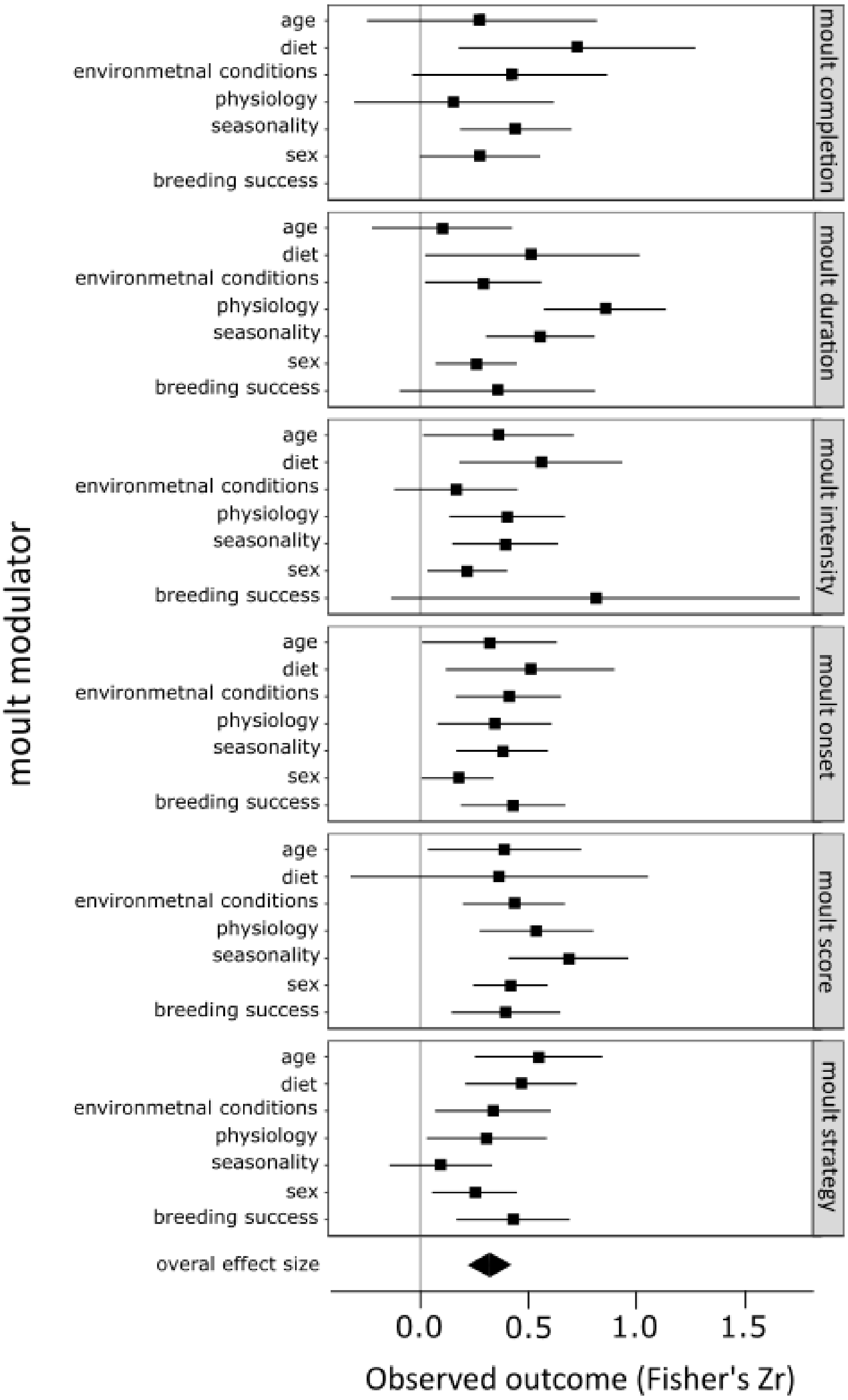


Figure 5. Funnel plot of effect sizes (Fisher's Zr) standard error plotted against their corresponding sampling variance. The continuous line represents the meta-analytic mean. Dotted lines depict 95% confidence intervals.

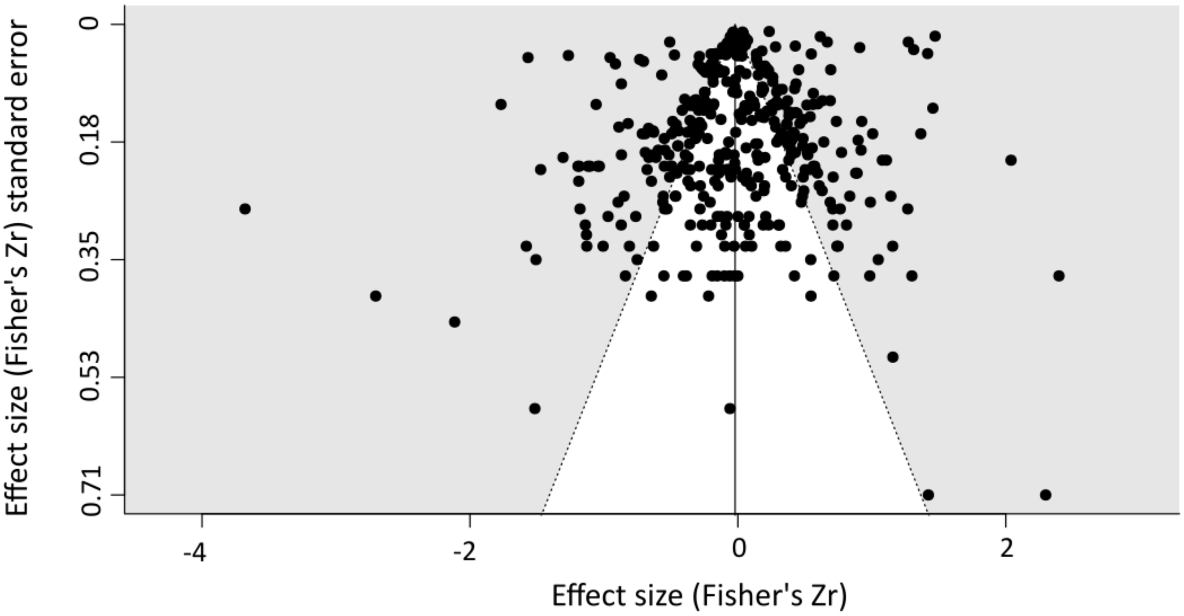
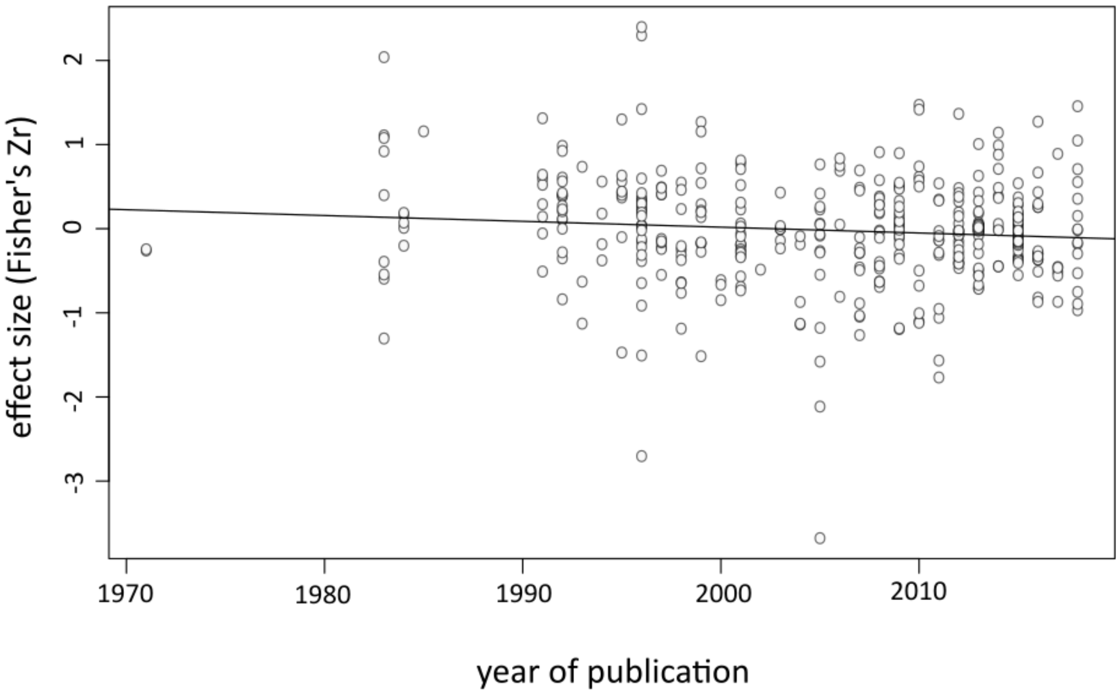


Figure 6. The overall published effect size over time. The solid black line represents the model estimate.



TABLES

Table 1. Categorization of moderator variables included in the analyses. Each general broad variable was divided into specific traits

Variable	Specific trait
Study ID	-
Study type	Observational / experimental
Sex	Male / female / not distinguished
Age	Juvenile / adult / not distinguished
Data source	Raw data / extracted from linear model
Geographical location	Cold-temperate / subtropical-tropical / widespread
Developmental mode	Altricial / precocial
Breeding type	Cooperative / non-cooperative
Family living	Present / absent
Food preferences	Generalist / specialist
Habitat preferences	Generalist / specialist
Migratory status	Migrant / sedentary
Response variable	Moult onset / moult intensity / moult rate / moult completion / moult score / moult strategy
Moult modulator	Age / sex / breeding success / breeding time / climate / environmental condition / seasonality / physiology / immunology / diet

Table 2. Categorization of response and explanatory variables included in the analyses. The variables were recorded as described in the original publications and then grouped into broad categories (specific trait)

Variable	**Specific trait**	**Examples of traits within category**
response variable	moult completion	moult termination moult end date complete moult moult closing date
	moult duration	duration of feather renewal duration of primaries moult
	moult intensity	advancement of moult increase in moulting score inflection point moult speed number of primaries replaces interval between moults
	moult onset	moult initiation moult start date
	moult score	moult score moult stage
	moult strategy	age at moult onset moult asymmetry moult investment moult timing period of moults
moult modulator	age	age age classes
	breeding success	age of partner breeding status brood size nestling mass
	breeding time	breeding cycle date of incubation date of last egg reproduction onset
	climate	date of 50% snow cover

		rainfall pattern average temperature wet vs. dry season
	diet	food availability food restriction food supplements
	environmental conditions	colony location habitat quality light exposition temperature urbanization
	immunology	infection status immune challenge immunization
	physiology	body mass body condition fat score testosterone level total oxidant status
	seasonality	calendar date day length photoperiod
	sex	sex

Table 3. Final model results for directional effect size generated in ASReml-R using a linear mixed-model approach

Moderator variable	*df*	Denominator *df*	*F*	*P*
Intercept	1	45.6	0.509	0.479
Study type	1	263.6	12.530	0.013
Sex	2	315.9	0.380	0.955
Age	2	298.0	5.692	0.173
Moult modulator	9	298.7	1.814	0.053
Response categories	5	325.4	1.232	0.294
Moult modulator x response categories	36	303.1	1.883	0.002

Table 4. Final model results for absolute magnitude of the effect size generated in ASReml-R using a linear mixed-model approach

Moderator variable	*df*	Denominator *df*	*F*	*P*
Intercept	1	94.7	60.98	<0.001
Study type	1	424.5	17.08	0.209
Sex	2	395.1	0.21	0.677
Age	2	450.7	1.44	0.233
Moult modulator	9	378.1	4.15	<0.001
Response categories	5	471.7	1.70	0.409
Geographical location	2	61.5	0.56	0.541
Moult modulator x response categories	40	428.6	1.91	<0.001
Moult modulator x geographical location	13	376.4	2.24	<0.01