



# Sex-dependent elevational effects on bird feather moult

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## Abstract

Environmental conditions, including weather, influence organisms in a variety of ways. Specifically, animal males and females might be affected differently by ambient temperatures that vary in time and space. In this study, we explored the effect of elevation, which strongly determines ambient temperatures, on the speed of moult of the wing's flight feathers in the Eurasian Blackbird (*Turdus merula*). Differences in moult speed may alter the wing's surface area during the moulting process and hence may influence flight performance, including the ability to escape from predators. Sampling elevations were categorized to locations > 1000 m above mean sea level (AMSL) and locations < 300 m AMSL. We found that birds moulted their primary wing feathers faster at low elevations than at high elevations. In addition, differences in elevation-related moult speed were modulated by bird sex. Males moulted their primary feathers faster than females at high elevations but slower than females at low elevations. Our findings highlight the importance of considering sex-dependent responses to spatial environmental conditions, which may influence key properties of major annual-cycle activities and life-history processes.

**Keywords** Environmental gradients · Eurasian Blackbird · Life-history transitions · Scheduling of physiological processes · Thermal environment

## Introduction

Males and females of both plants and animals often differ in behavioral, physiological, ecological, morphological and chromatic characteristics (Van Haaren et al. 1990; Andersson 1994; Grant et al. 1994; Kaciuba-Uscilko and Gruzca 2001; Dale et al. 2015). Specifically, differences between males and females in thermoregulation or response to ambient temperatures have been described in numerous studies (Cunningham et al. 1978; Wagner and Horvath 1985; Yang and Gordon 1996; Kaciuba-Uscilko and Gruzca 2001; Winne and Keck 2005). In general, males prefer lower ambient temperatures compared to females and have a higher tolerance for lower temperatures than females (Karjalainen 2012; Schaudienst and Vogdt 2017). As a result of these differences, sex-specific selection of habitats

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takes place during non-breeding periods among many species, especially in highly mobile ones, such as bats (Levin et al. 2013) and birds (Chapman et al. 2011). In these species, males tend to prefer habitats characterized by lower temperatures compared to those preferred by females (Alonso et al. 2009; Chapman et al. 2011; Levin et al. 2013). Sexual differences in thermoregulation and response to ambient temperatures may consequently influence various physiological processes such as bird feather moult, but these effects have only been rarely studied to date.

Feather moult is an important and physiologically demanding life-history process that involves the replacement of plumage due to natural wear and tear (Lindström et al. 1993; McNamara and Houston 2008; Jenni and Winkler 2020a, b). In order to maintain the functionality of their plumage, passerine birds usually replace their entire plumage annually. Since feathers cannot be renewed continuously from their base, like other keratinous structures (e.g., hair and claws), they are replaced only after the shedding of old feathers. The time lag between feather shedding and the full growth of the new feather creates a feather gap. Because several adjacent feathers may be shed during a short time interval, feather gaps of various widths and lengths are usually created during the moult process (Ginn and Melville 1983; Swaddle and Witter 1997; Jenni and Winkler 2020a, b). The speed of the moult process, and therefore also the size of the feather gap, is largely determined by the number of feathers that have been shed within a short time interval (Rohwer and Rohwer 2013). Since rapid moults create large feather gaps compared with slower moults that result in small gaps, moult speed has the potential to substantially affect numerous physiological and behavioural costs, including the wing's aerodynamic performance and associated costs of locomotion.

Moult-related feather gaps may substantially hamper flight performance and increase flight metabolism over periods of weeks to months (Haukioja 1971; Green and Summers 1975; Francis et al. 1991; Hedenström and Sunada 1999; Hedenström 2003). Since the size of the moult gaps may negatively affect a bird's flight capacity, there is a trade-off between the speed of the moult (and hence gap size) and flight performance that is important for foraging (Kiat et al. 2016b) and escaping from predators (Lind 2001). Notably, feather moult tends to be more rapid in more seasonal environments (Fogden 1972; Jenni and Winkler 2020b), or as a result of time constraints (Kiat et al. 2019a). Yet, the development of the feathers in the moult process (Swaddle and Witter 1994; Bortolotti et al. 2002), and likely also the moult rate, also depend on the availability of food resources (Wiersma and Verhulst 2005) and the physiological ability of the bird to utilize these resources. Therefore, we expect that bird physiology will depend on environmental conditions, including ambient temperature, which could affect the rate of feather moulting. However, empirical evidence is scarce regarding the influence of both external factors such as ambient temperature, and internal factors such as bird sex, on the speed of feather moult (but see Grubb Jr et al. 1991).

In this study we aimed to explain within-species variation in feather moult speed. We specifically tested for an effect of elevation-dependent ambient temperature and whether an individual's sex modulated the response to this environmental gradient during the moulting period. We hypothesize that differences between males and females in environmental temperature preferences could affect physiological processes and that, specifically, bird feather moult may vary between the sexes at different ambient temperatures (e.g., Kiat et al. 2019b). We predict that birds found in locations where thermal conditions are more suitable for them will moult faster and therefore that moulting speed will change due to the difference in ambient temperature associated with elevation. Moreover, based on the documented differences between the sexes in their thermal tolerance (Alonso et al. 2009;

Chapman et al. 2011), we predict that males will moult more rapidly than females at higher elevations and more slowly than females at lower elevations. We tested our predictions in Eurasian Blackbirds (*Turdus merula*) undergoing active wing-feather moult after their breeding at two elevation ranges in Israel using wing primaries gap size as a proxy of moult speed.

## Methods

To test the effects of elevation, which is tightly correlated with ambient temperatures (Fig. S1), and sex on feather moult speed, we collected wing moult data from the Eurasian Blackbird. This species is a common, sexually dimorphic passerine that occurs across a broad range of elevations. In Israel, the Eurasian Blackbird is a sedentary species, although some local movements, mainly to lower altitudes, occur in mid-winter (Collar and Christie 2019). During 2012–2019 we sampled birds with an active post-breeding primary feather moult in different sites across Northern and Central Israel. All sampling sites (Fig. S2) were located within two elevational ranges, (1) high, at locations 1000–1600 m above mean sea level (AMSL): Mt. Hermon (33.31° N/35.77° E), Senaim Wadi (33.27° N/35.73° E) and Odem Forest (33.20° N/35.77° E), and (2) low, at locations –400–300 m AMSL: Kfar Yuval (33.24° N/35.59° E), Regba (32.98° N/35.11° E), Mt. Carmel Slopes (32.69° N/34.99° E), Soreq Valley (31.77° N/34.92° E), Modiin Hills (31.90° N/34.99° E) and Einot Tzukim Nature Reserve (31.72° N/35.45°). The habitat in these sites is Mediterranean woodlands, orchards, and tamarisk groves (*Tamarix* sp.), or a combination of those. The birds were trapped using mist-nets (permit number A258, Israel Nature and Parks Authority) and the sex of each individual was identified using diagnostic characteristics. Males have entirely black plumage and a yellow or orange-yellow bill, and females are duller dark brown with a brownish bill and some dull yellow around its base (Collar and Christie 2019).

The active moult state of each of the ten primary feathers ( $P_1 - P_{10}$ ) was recorded during the post-breeding moult period (late June to early September, mainly July–August) using a moult scale of 0–5 (Ginn and Melville 1983) as shown in Table 1. Then, we estimated the missing proportion of each feather (for moult scores 1–4), while for moult scores of 0 and 5 (fully grown old and new feathers, respectively), the gap length was 0.00 (Table 1). Due to differences in the lengths of different primary feathers (Underhill and Joubert 1995), we measured the length of each primary feather for a subset of individuals (Table 2). The sum of these mean feather lengths in the Eurasian Blackbird is 908.3 mm, representing the lengths of the primary feathers of a complete wing that is not undergoing active moult. We then used moult data to calculate the missing feather lengths due to moult. For example, for an individual with moult scores of 5-4-4-4-3-1-0-0-0-0 (Fig. 1), the feather gaps are 0.0, 23.3, 23.5, 24.3, 51.5, 105.7, 0.0, 0.0, 0.0 and 0.0 mm, respectively. For this individual, the total gap length is 228.3 mm, which represents 25.1 % of the value of a non-moulted wing. To reliably study birds during active primary moult, we calculated the gap size only for individuals with a fully grown or almost fully grown  $P_1$  (moult score = 4 or 5) and an old or missing  $P_{10}$  (moult score = 0 or 1), but not growing or fully grown  $P_{10}$  (moult score = 2 to 5) This was done to avoid calculating a biased estimate of the primary moult speed in cases in which the feather gap is not confined within the surface of the wing's ten primary feathers. Importantly, the moult gap size is highly correlated with the speed of moult,

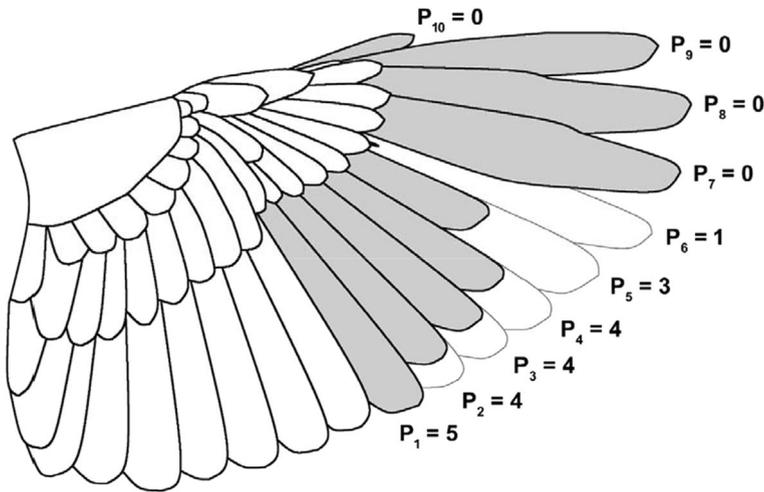
**Table 1** Description of primary moult scores used in this study (Ginn and Melville 1983) and estimated proportions of the missing feather lengths from a complete wing

| Moult score | Description  | Estimated proportion of the missing feather length |
|-------------|--|--|
| 0           | A remaining old feather  | 0.00   |
| 1           | A missing old feather or a new feather that is found completely within its pin   | 1.00   |
| 2           | A new feather just emerging from its sheath up to the length of one third of a fully grown feather                         | 0.75   |
| 3           | A new feather with a length between one and two thirds of a fully grown feather  | 0.50   |
| 4           | A new feather that is more than two thirds the length of a fully grown feather and with remains of waxy sheath at its base | 0.25   |
| 5           | A new, fully developed feather with no traces of remaining waxy sheath at its base   | 0.00   |

**Table 2** The lengths of the Eurasian Blackbird primaries

| Feather         | Mean length (mm) | Standard deviation (mm) |
|-----------------|------------------|-------------------------|
| P <sub>1</sub>  | 91.7             | 6.7                     |
| P <sub>2</sub>  | 93.0             | 7.2                     |
| P <sub>3</sub>  | 94.0             | 6.2                     |
| P <sub>4</sub>  | 97.0             | 5.3                     |
| P <sub>5</sub>  | 103.0            | 6.1                     |
| P <sub>6</sub>  | 105.7            | 5.5                     |
| P <sub>7</sub>  | 103.7            | 4.7                     |
| P <sub>8</sub>  | 100.7            | 3.8                     |
| P <sub>9</sub>  | 88.7             | 2.9                     |
| P <sub>10</sub> | 31.0             | 2.6                     |

mean ± standard deviation of the length of the part that protrudes from the skin; n = 3 individuals



**Fig. 1** Example of a hypothetical moult score which includes primary moult scores of 5-4-4-4-3-1-0-0-0-0, and a feather gap created by the growing and shedding of primaries P<sub>2</sub>–P<sub>6</sub> that constitute 25.1% of the total feathers lengths of the entire primary feathers of the wing

allowing estimation of moult speed by a single sampling of each individual (Bensch and Grahn 1993; Rohwer and Rohwer 2013).

Using a generalised linear model (GLM; family=Gaussian;  $g(\mu) = \mu$ ), we explored the effects of elevation (two categories: high > 1000 m AMSL and low < 300 m AMSL), sex (male or female) and their interaction (independent variables) on moult speed, which is measured as the wing's primaries gap size (dependent variable; normally distributed,  $P=0.329$ , Shapiro-Wilk test). Due to the change in the shape of the moult gap with the progression of the moult process, we also included in the model the stage of the primary moult, represented by the number of new and full-grown primaries (Bensch and Grahn

1993). Furthermore, we included the ordinal date of the sampling of each individual to account for a possible effect of the progression of the season on moult gap size. The analysis (two-tailed, critical  $\alpha=0.05$ ) was performed using the package ‘*lme4*’ (Bates et al. 2012) in R (version 3.6.1).

We note that in Israel, and hence also in the nine locations where Blackbirds were sampled in this study, there is a high correlation between elevation and latitude (Pearson correlation  $r=0.81$ ). Due to this high correlation we did not include latitude as an explanatory variable in our analysis. However, in order to examine the effects of these two factors (elevation vs. latitude), we tested the same GLM described above but included latitude instead of elevation. We then selected the best model using AICc (Akaike 1987; Barton 2012).

## Results

We collected primary feathers’ moult data and calculated the primaries’ moult-related wing gap size for 76 Eurasian Blackbirds that were divided into four groups: (1) males trapped in low areas (mean moult gap size  $\pm$  standard deviation,  $171.6 \pm 46.9$  mm;  $n=17$ ), (2) males from high areas ( $160.6 \pm 54.3$  mm;  $n=29$ ), (3) females trapped in low areas ( $216.6 \pm 63.3$  mm;  $n=10$ ) and (4) females from high areas ( $143.9 \pm 52.2$  mm;  $n=20$ ). The GLM results ( $r^2=0.51$ ,  $df=7$ ; Table 3) indicated that trapping site elevation, bird sex and their interaction, and the stage of the moult significantly affected moult gap size, and thus moult speed, in the Eurasian Blackbird. The moult gap size was higher in low areas ( $<300$  m AMSL) than in high areas ( $>1000$  m AMSL), and the primary moult speed became slower with the progression of the moult process (Table 3). In addition, females moulted their primary feathers more rapidly than males in low elevations, but more slowly than males in high elevations (Fig. 2). Ordinal date did not affect the moult gap size (Table 3).

The comparison between the GLMs that included elevation as an explanatory factor and those that included latitude showed stronger support ( $\Delta\text{AICc}=5.96$ ) for the model with elevation (AICc=790.27, log-likelihood = -387.32, weight=0.95) over latitude (AICc=796.23, log-likelihood = -390.29, weight=0.05).

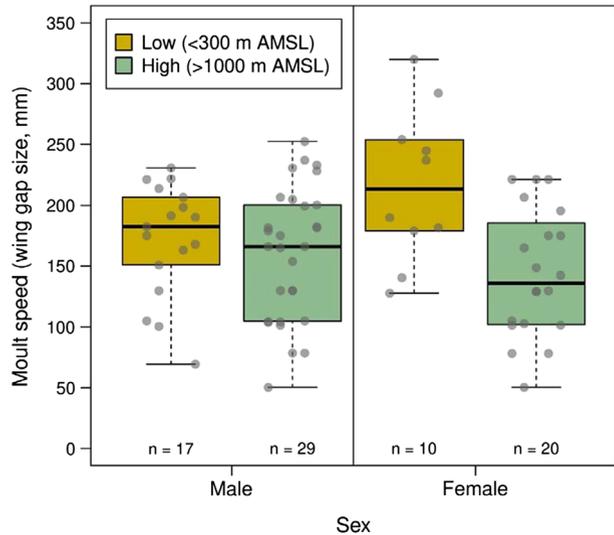
## Discussion

Feather moult is an important process in the avian yearly cycle (Jenni and Winkler 2020a, b) that nonetheless may have short-term, negative consequences of reduced wing surface area and consequently hampered flight performance (Hedenström 2003). In this

**Table 3** The effects of elevation (meters above mean sea level), sex, moult stage, and ordinal date on moult gap size among Eurasian Blackbirds: list of statistics for the tested independent factors

| Factor                        | Coefficient $\pm$ standard error | <i>t</i> value | <i>P</i> value |
|-------------------------------|----------------------------------|----------------|----------------|
| Elevation                     | $48.16 \pm 16.32$                | 2.95           | 0.004          |
| Sex <sub>male</sub>           | $26.24 \pm 12.20$                | 2.15           | 0.034          |
| Elevation:sex <sub>male</sub> | $-50.92 \pm 20.38$               | -2.50          | 0.015          |
| Moult stage                   | $-16.73 \pm 2.91$                | -5.75          | <0.001         |
| Sampling ordinal date         | $0.09 \pm 0.41$                  | 0.23           | 0.819          |

**Fig. 2** The effects of elevation (two categories: >1000 m above mean sea level, AMSL and <300 m AMSL) and bird sex on the speed of moult in the Eurasian Blackbird (*Turdus merula*; n = 76 individuals). The results indicate that moult speed is higher in lower areas and that females moulted faster than males in lower areas and slower than males in higher areas



study, we found that Eurasian Blackbirds moulted their flight feathers more slowly at high elevations than at low elevations, resulting in smaller reduction of wing surface area and consequently possibly smaller effects for flight performance during moult in higher elevations. Additionally, we found that the differences in the speed of moult between high and low elevations depended on the individual's sex. Males moulted their flight feathers faster than females at high elevations, but slower than females at low elevations (Fig. 2).

We propose that between-sex differences in the speed of moult, which result in different wing morphologies during the moulting period at different elevations, could result from sex-specific thermal preference or tolerance. In contrast, a previous experiment that examined the effect of ambient temperature during moult did not find that temperature affected feather growth rate (Viain and Guillemette 2016). Nonetheless, testing the physiological mechanisms by which temperature influences feather moult, including between-sex differences, could be a promising future direction. We note that several other environmental variables are known to change with elevation, including oxygen partial pressure, which could also possibly impact the physiological tolerance of the animals (Altshuler 2006, Altshuler and Dudley 2006, DuBois et al. 2017). Yet, oxygen partial pressure is not expected to have an effect on the birds in the elevations sampled in the present study (< 1600 m AMSL).

The speed of feather moulting strongly affects the duration of the process – moult will be completed sooner if more flight feathers are shed and grow simultaneously within a short time interval. Rapid moult may nevertheless substantially reduce flight performance, hampering the ability to escape a predatory attack and inducing elevated flight metabolism (Hedenström and Sunada 1999; Lind 2001; Hambly et al. 2004). When the moult is slow, the wing's moult gap is present for a longer time, although the size of the gap is smaller (Jenni and Winkler 2020b). Therefore, there are trade-offs between moult speed and the total duration of the process; rapid moult is short but involves large moult gaps, whereas prolonged moult is characterized by having a small gap throughout a substantial part of the bird's annual cycle. The latter strategy is rare among temperate species, but often adopted by tropical birds (Fogden 1972).

Aerodynamic measurements of various wing morphologies, including wings with variable moult gap sizes (Achache et al. 2018), may help reveal the biomechanical consequences of rapid versus slow moulting in various species, between the two sexes and under various moulting environments. While the biomechanical consequences of these wing morphologies are not well understood, our study demonstrates that the combination of environmental heterogeneity and the individual's sex creates specific changes in bird form, and possibly function, with possible consequences for bird fitness (Arnold 1983). Accordingly, males and females likely differ in their ability to escape predators and in their energetic requirement during the period of feather moulting in a given environment due to the difference in their wing shapes. Specifically, the size of the moult gap, which is influenced by the environmental conditions they experience during this period, could be a major influencing factor. These sexual differences in moult gap size may lead to variation in compensation mechanisms that may help the bird to avoid predation (Lind 2001), by undertaking various behavioural and physiological changes (Cresswell 2008). Furthermore, different escape capacities due to sex-specific wing morphology may result in differential survival (Liker and Székely 2005), with consequences for population structure and demography (Székely et al. 2014).

Additional factors that may affect the speed of moult are the amount of resources that a bird is able to acquire for the moulting process (Wiersma and Verhulst 2005) and the time available for completing this process. Juvenile birds, characterised by less efficient foraging (Marchetti and Price 1989; Wunderle 1991), moult slower than adults (Kiat and Izhaki 2016a). In addition, northern breeding distribution and long-distance migration, both associated with shorter time available for moulting, have been found to increase the speed of moult compared with southern or sedentary species, respectively (Fogden 1972; Green and Summers 1975; Francis et al. 1991; Kiat et al. 2019a). Northern populations, which moult their plumage in more seasonal environments, are also associated with lower adult survival compared with those in less seasonal environments, for example, in tropical regions (Ricklefs 1997).

Environmental changes along elevational gradients are known to influence the morphology, ecophysiology, growth and development, survival, reproduction and spatial distribution of many organisms (Hammond et al. 2001; Hodkinson 2005; Pellissier et al. 2012; Castiglione et al. 2017; Hao et al. 2019; Scholer et al. 2019). The response of organisms to environmental changes across elevational gradients might offer insights regarding how species may respond to temperature shifts associated with global climate change in time (Hodkinson 2005) since in both scenarios, individuals are exposed to different ambient temperatures that may affect different physiological processes, including feather moulting (e.g., Kiat et al. 2019b). Previous studies have shown an impact of environmental warming on the timing of feather moulting (Jukema and Wiersma 2014; Tomotani et al. 2018). Furthermore, global warming can affect the extent of feather moult differently in males and females among passerine species, including the Eurasian Blackbird (Kiat et al. 2019b). Therefore, global warming might also affect the speed of feather moult, with possible sex-specific consequences. We thus call for future exploration of this potential effect.

By demonstrating the effects of elevation and bird sex on a major avian-annual routine process, our study highlights the importance of linking environmental conditions to life-history transitions, annual routines and dynamic animal morphology. We propose that males and females may respond differently to environmental heterogeneity over various axes, including elevational, latitudinal, longitudinal and temporal gradients. These ecological effects are important for better understanding evolutionary and life-history processes (Schoener 2011).

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**Author contributions** YK and NS conceived the study. YK collected the data and performed the analyses. NS advised the analyses. YK wrote the manuscript and NS contributed to manuscript writing.

**Data availability** The data are provided as supplementary material.

**Declarations**

**Conflict of interest** The authors declare no conflicts of interest.

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