

Recent changes in allometric relationships among morphological traits in the dipper (*Cinclus cinclus*)

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Abstract Organisms are responding to recent climate warming by changing different aspects of their biology, including morphology. The present work examines the way in which dipper (*Cinclus cinclus*) morphology has varied over the past 20 years (1985–2005) in Sierra Nevada (south-eastern Spain). Tarsus length has decreased, but wing and tail length have increased in the same period. These opposite trends have provoked changes in the allometric relationships among the different parts of the body in the dipper. A decrease in body size is predicted by Bergmann's rule, and similar results have been found in other birds. However, although this study found a decrease in tarsus length, no change was found for body mass. The increase in wing and tail length may be related to a variation in the trophic niche in response to the decrease in water volume of rivers that occurred during the study period. Other studies show that the dipper's diet varies with water flow, and water flow has decreased in the study area as a consequence of climatic warming.

Keywords Allometry · *Cinclus cinclus* · Climatic change · Dipper · Morphology

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Introduction

Currently, the Earth is undergoing a global warming [Intergovernmental Panel on Climate Change (IPCC) 2001], and because many biological and ecological traits of organisms are temperature-dependent, this climate change will provoke certain predictable changes (Hughes 2000; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2004). For birds, climate warming has been related to phenological changes in laying date (Crick et al. 1997) and migration (Cotton 2003), changes in clutch size (Møller 2002), changes in distribution (Thomas and Lennon 1999) and in population dynamics (Sæther et al. 2000), and even, changes in breeding success (Sanz et al. 2003).

Morphological changes in response to climate warming are also predictable. Bergmann's rule establishes that endothermal animals have a smaller body size in regions with higher environmental temperature, because the greater the body surface (smaller body size) the higher the heat dissipation, this being advantageous in warm climates, while a smaller body surface (larger body size) results in lower heat loss, this being advantageous in cold climates (Margalef 1995; Millien et al. 2006). Therefore, as temperature increases, birds may respond to climatic change by decreasing body size. Indeed, in many bird species, body size has diminished in recent years (Yom-Tov 2001; Yom-Tov et al. 2006). On the other hand, Allen's rule establishes that, in warm climates, endotherm animals have longer extremities, increasing their body surface (greater heat dissipation), and the reverse occurs in cold zones (Margalef 1995). For this reason, global warming could alter allometric relationships among traits in animals. Yom-Tov et al. (2006) found some evidence in favour of Allen's rule in 14 bird species of the UK.

Besides temperature, other factors (related or not to climate change) may also provoke directional morphological changes (Millien et al. 2006). For example, body size has increased during the past few decades in the blackbird (*Turdus merula*), two species of rodents (*Apodemus speciosus* and *Eothenomys smithii*), and two species of frogs (*Rana ridibunda* and *R. lessonae*), these changes being related to an increase in food availability as a consequence of climate change (Yom-Tov and Yom-Tov 2004; Tryjanowski et al. 2006; Yom-Tov et al. 2006). Analogously, morphological variation in goshawks (*Accipiter gentilis*) has been attributed to a variation in their diet (Tornberg et al. 1999; Yom-Tov and Yom-Tov 2006). Higher temperatures have provoked lower fat reserves for night in the great tit (*Parus major*) (Gosler 2002). Jakober and Stauber (2000) related a decrease in wing length in the red-backed shrike (*Lanius collurio*) to an increase in environmental variability.

In this work we analyse the morphological variations in the dipper (*Cinclus cinclus*) from 1985 to 2005 in a mountain of south-eastern Spain (Sierra Nevada). During the study period, temperature has increased in this zone (Moreno-Rueda et al. manuscript submitted), and, therefore, morphology may have changed in this population in response to climatic change. Because Bergmann's rule predicts a reduction in body size, while Allen's rule predicts a lengthening of extremities, we expect a variation in allometry in response to recent climate change.

Methods

The dipper is a passeriform adapted to fluvial environments, where it is a specialist, making it very sensitive to environmental change (Tyler and Ormerod 1994). In Spain, it is a sedentary species associated primarily with mountain rivers and streams (López Alcázar et al. 2003). The study was performed in Sierra Nevada, the highest mountain in the Iberian Peninsula [3,482 m above sea level (a.s.l.)], covering about 140,000 ha. We sampled the Genil River (82.8% of the sample size) and its tributaries.

The study was performed between 1985 and 2005, both years inclusive (no sampling in 1998). Dippers were captured with mist nets (with the pertinent permission) over the entire year. We considered only adults and sedentary individuals, excluding immature and immigrant dippers from analyses. We measured tarsus and beak length with a calliper (accuracy to 0.01 mm), tail and wing length with a ruler (accuracy 0.5 mm), and body weight with a balance (accuracy 0.1 g), and the third primary for sexing. All individuals were measured by the same researcher (J.M.R.). Body mass significantly varied with the month

($F_{11,310} = 2.83$; $P = 0.001$), and, for this reason, we used the residuals of body mass controlled for by month. The remaining traits measured did not show significant changes with month (always $P > 0.10$). In the 20 years of the study, we captured 454 adult individuals, 243 males and 211 females. For sexing, we used the formula of Campos et al. (2005b) for southern Spain, which gives an error of only 1.3%. This formula uses weight and the third primary length to sex birds. Although morphology changed with years (Results section), there was no overlap between sexes for the traits used in sexing. We captured an average of 22.7 (\pm SD = 21.1) individuals per year, with a median of 19.5, and a range of 3–89 individuals per year. The mean altitude of the captures was 1,003 (\pm SD = 266) m a.s.l. (median = 900 m), with a range of altitudes of 700–2,500 m a.s.l. Annual mean altitude of captures varied directionally with the years ($r = 0.48$; $P < 0.05$; $n = 20$); therefore, we statistically controlled for altitude in the analyses. Data on climate and stream water flow were taken from the Regional Government of Andalusia.

Data showed a distribution close to normal, and parametric statistics were used (Sokal and Rohlf 1995). Some data were lost or could not be taken, varying the sample size among analyses. We calculated the allometric relationships between tarsus and residual mass (Mass/Tarsus), wing and residual mass (Mass/Wing), and tarsus and wing (Wing/Tarsus). For the two first cases, inasmuch as mass varies with the linear measurements of the wing and tarsus according to a cubic function, we estimated the allometry using the residuals of the regression of the tarsus or wing, respectively, on the mass, with all variables log-transformed (Jacob et al. 1996), and with month introduced as covariate. The relationship between wing and tarsus (Wing/Tarsus) was estimated by division of the wing length by the tarsus length. Sexual dimorphism for each year was calculated as the mean value for males divided by the mean value for females.

Because sexual dimorphism is apparent in the dipper (e.g., Campos et al. 2005b), males and females were analysed separately. We used Pearson's product-moment Pearson correlation (r) to establish the relationships among morphological traits and to examine the variation of traits with years, controlling for mean altitude for each year (partial correlations, r_{partial}). Inasmuch as the sample size varied among years, years with larger sample sizes presumably gave a more accurate average population value for morphometry than did years with a small sample size. For this reason, we calculated a new coefficient of correlation weighting for sample size, denoted as r' (controlling for mean altitude). This statistic diminished the error associated with years with low sample size. Values of P were corrected by the Bonferroni sequential method (Sokal and Rohlf 1995). However, because Bonferroni correction is restrictive

and sample size was small in some analyses, there was a high risk of type I statistical errors (Moran 2003; Nakagawa 2004), so that, when we used the Bonferroni correction, we used a value of $\alpha = 0.10$ (Chandler 1995).

Results

Allometric relationships among the traits measured

Table 1 shows the mean \pm standard deviation of morphological data throughout the study for male and female dippers. Wing and tail length, the two traits determined by feathers, were correlated (marginally in females after the Bonferroni correction) (Table 2). For males, residual mass (controlling for seasonal variation) was correlated with tarsus and wing length, but not for females (Table 2). Beak and wing length were also correlated (Table 2).

Table 1 Mean \pm SD (sample size) of morphological measurements for males and females dippers in the study area

Trait	Males	Females
Wing length (mm)	95.9 \pm 2.27 (196)	88.3 \pm 1.96 (180)
Beak length (mm)	24.7 \pm 1.48 (104)	23.3 \pm 1.35 (99)
Tarsus length (mm)	30.8 \pm 0.86 (130)	29.0 \pm 0.95 (132)
Tail length (mm)	54.6 \pm 5.49 (39)	49.7 \pm 4.24 (45)
Body mass (g)	65.7 \pm 4.63 (175)	55.2 \pm 4.07 (147)

Table 2 Allometric relationships among morphological traits for males (upper-right half) and females (lower-left half). Values of r_{partial} and sample size (n) are shown. Correlations that were significant after the Bonferroni correction ($k = 10$) are shown in *bold type*

Trait	Wing	Beak	Tarsus	Tail	Residual mass
Wing		$r = 0.27^{**}$ $n = 96$	$r = 0.02$ $n = 122$	$r = 0.64^{***}$ $n = 32$	$r = 0.21^{**}$ $n = 149$
Beak	$r = 0.26^*$ $n = 89$		$r < 0.01$ $n = 93$	$r = 0.27$ $n = 21$	$r = 0.07$ $n = 86$
Tarsus	$r = 0.11$ $n = 121$	$r = 0.09$ $n = 85$		$r = -0.15$ $n = 29$	$r = 0.27^{**}$ $n = 112$
Tail	$r = 0.43^*$ $n = 35$	$r = 0.24$ $n = 21$	$r = 0.11$ $n = 32$		$r = 0.01$ $n = 29$
Residual mass	$r = 0.01$ $n = 126$	$r = -0.02$ $n = 72$	$r = 0.1$ $n = 94$	$r = -0.14$ $n = 32$	

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

Morphometric variation with years in the dipper

Males and females showed morphological variations in similar directions, although correlations were usually stronger in males (Table 3). In fact, sexual dimorphism did not vary significantly during the study period (Table 3). For males (but not significantly for females), there was a significant decrease (when data were weighted by sample size) in tarsus length (Table 3). In contrast, there was an increase in wing and tail length, showing a similar size of effect, with the advance of years (the correlations, again, were not significant for females) (Table 3).

These findings imply that, in general (and at least for males), the traits measured varied during the study period, but in opposite directions, and, therefore, the allometric relationships among them must also have varied. The relation between mass and tarsus (Mass/Tarsus) did not vary significantly during the study (Table 3). The relationship between mass and wing length (Mass/Wing) did not vary, either, during the study (Table 3). Lastly, the Wing/Tarsus ratio increased during the study period (Table 3; Fig. 1), implying that dippers now have longer wings, with respect to their tarsus, than they had 20 years ago.

Climatic variation during the study period

The mean annual temperature increased in south-eastern Spain between 1983 and 2004 by about $1.47 \pm 0.63^\circ\text{C}$, during the study period ($F_{1,378} = 4.28$; $P < 0.05$; $\beta = 0.07 \pm 0.03$; meteorological station introduced as random factor: $F_{97,378} = 13.83$; $P < 0.001$; Moreno-Rueda et al. manuscript submitted). Moreover, there was a trend for a reduction in water flow in Sierra Nevada mountain streams, especially acute in the Genil River, where most of the dippers were caught (Fig. 2).

Discussion

The results show that the tarsus length of the dipper has diminished in the past 20 years. This would agree with the predictions based on Bergmann’s rule, by which endotherm animals are expected to respond to the climate warming by a body-size reduction (Millien et al. 2006). Indeed, temperature has increased during the period of time considered here, on global, regional and local scales (Jones et al. 1999, 2001, this study). Nevertheless, body mass did not decrease during the study period. Moreover, Campos et al. (2005a), by comparing some mountain populations, concluded that Bergmann’s rule does not apply to the dipper. While Bergmann’s rule is applicable to most non-migratory passerines (Ashton 2002; Meiri and Dayan 2003), selective

Table 3 Variation in morphology in the dipper in Sierra Nevada during the study period. The Pearson's product-moment correlation (r_{partial}), the correlation weighted by sample size for each year (r'),

and the sample size are shown. The correlations significant after the Bonferroni correction ($k = 8$; 4 for dimorphism) are shown in *bold type*

Variable	Males			Females			Dimorphism		
	r_{partial}	r'	n	r_{partial}	r'	n	r_{partial}	r'	n
Wing	0.68**	0.73**	19	0.31	0.51*	19	0.23	0.09	18
Beak	-0.33	0.18	13	0.44	0.18	10	-0.11	0.07	9
Tarsus	-0.56*	-0.69**	15	-0.08	-0.39	17	-0.24	-0.11	14
Tail	0.88**	0.79*	8	0.08	0.46	9	-	-	4
Residual mass	0.14	0.16	19	-0.04	-0.20	19	0.34	0.34	18
Mass/Tarsus	0.13	0.21	15	0.01	-0.10	14			
Mass/Wing	-0.26	-0.36	18	-0.14	-0.18	17			
Wing/Tarsus	0.74**	0.79**	15	0.68**	0.28	17			

* $P < 0.05$

** $P < 0.01$

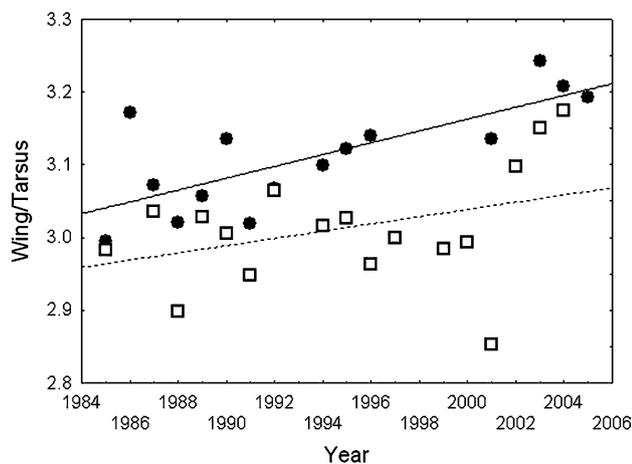


Fig. 1 Allometric changes between wing and tarsus in the dipper during the last 20 years. Males *black circles and solid line*; females *white squares and broken line*

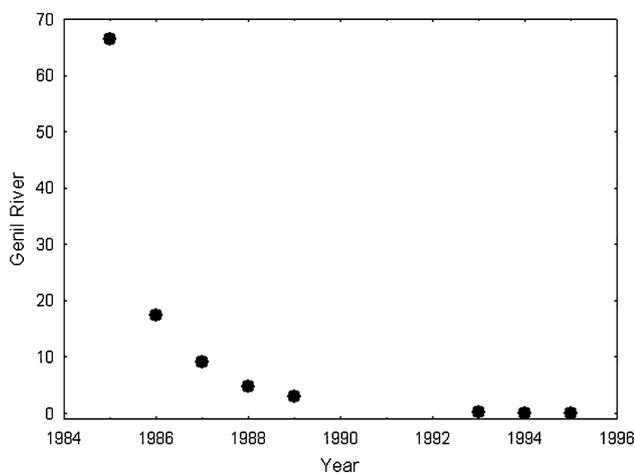


Fig. 2 Water flow in the Genil River during the study period

factors other than temperature may affect body size in this species, giving rise to the results reported by Campos et al. (2005a). For example, body size in *Sorex* shrews is regulated primarily by the size of their prey, and, because prey sizes diminish with latitude, these species do not conform to Bergmann's rule (Ochocińska and Taylor 2003). Climate change seems to affect other traits in the dipper, such as population dynamics and laying date (Sæther et al. 2000; Hegelbach 2001), and it affects body size in several passerines (Yom-Tov 2001; Yom-Tov et al. 2006), but results here do not support the idea that body size has significantly varied in response to climatic change in this species. Why tarsus length has decreased in the past 20 years remains obscure.

The findings of this study hardly support the notion of an effect of the Allen rule on dipper morphology. Although some extremities (wing, beak and tail) were augmented in length, it is improbable that this was a consequence of the Allen rule, given that wing and tail are keratin-based structures that cannot dissipate heat. Moreover, tarsus length decreased instead of increasing. On the other hand, in the house sparrow (*Passer domesticus*), humerus and ulna are correlated with wing length (Johnston 1969). If this also applies to the dipper, the increase in wing length may be a consequence of Allen's rule in response to climatic warming. However, more direct measures would be necessary to resolve this issue.

Morphological changes in wing and tail may be better explained in relation to flight (e.g. Moreno-Rueda 2003). The change in beak morphology may be related to a change in the trophic niche (e.g. Grant and Grant 2002). Taylor and O'Halloran (2001) showed that dippers vary their prey and feeding method according to water flow, with more aerial insects consumed when dipping is hindered. In fact, the water flow has diminished in the study area during the

study period (Fig. 2, and R. Morales-Baquero, pers. com.). Water flow has also diminished in the Iberian Peninsula as a consequence of earlier snowmelt provoked by the climatic warming (Arnell and Liu 2001; Houghton 2004). On this basis, a possible explanation is that dippers have increased their feeding on terrestrial and/or aerial insects in the place of aquatic ones, responding to less water flow. Because wing and tail in the dipper are relatively short in order to dive (Tyler and Ormerod 1994), if dippers increase their feeding on non-aquatic species, there should be a selective pressure for longer wing and tail, and, perhaps, for a longer beak, too. Although the water flow decreased during the 1980s, it is probable that there was a lag in the evolutionary response by the dipper population, depending on genetic variability in morphology and time necessary for population turnover, explaining that the morphological change occurred in the 1990s. Similarly, Tornberg et al. (1999) described morphological changes in the goshawk (*Accipiter gentilis*) in a period of 37 years associated with changes in their primary prey. Microevolutionary changes in time periods such as the one in this study have been reported (e.g., Grant and Grant 2002).

Deficient nutrition affects body mass and osseous growth (tarsus) as well as feather growth (wing and tail) (e.g. Searcy et al. 2004); therefore, changes in nourishment cannot explain why some traits have decreased in size while others have increased.

In conclusion, different morphological traits of the dipper have varied in opposite directions during the past 20 years in Sierra Nevada (south-eastern Spain). To explain this pattern, we propose that lower water levels of rivers and streams where the dippers dwell have provoked a change in the trophic niche, causing an increase in wing, tail and beak length. At the same time, tarsus length has decreased for unknown reasons, varying allometric relationships in this species.

Zusammenfassung

Veränderungen allometrischer Verhältnisse zwischen morphologischen Merkmalen bei der Wasserramsel (*Cinclus cinclus*) in jüngster Zeit

Organismen reagieren auf die aktuelle Klimaerwärmung, indem sie verschiedene Aspekte ihrer Biologie inklusive morphologischer Merkmale ändern. Die vorliegende Arbeit untersucht, wie sich die Morphologie der Wasserramsel in der Sierra Nevada (SO-Spanien) über die letzten 20 Jahre (1985–2005) verändert hat. Der Tarsus hat sich verkürzt, wohingegen die Flügel- und Schwanzlänge im gleichen Zeitraum zugenommen haben. Diese gegenläufigen Trends

haben zu Änderungen der allometrischen Verhältnisse zwischen verschiedenen Körperteilen der Wasserramsel geführt. Laut der Bergmannschen Regel wird eine Reduzierung der Körpergröße prognostiziert, und ähnliche Körpergröße prognostiziert, und ähnliche Ergebnisse fanden sich bei anderen Vogelarten. Obwohl in der vorliegenden Arbeit jedoch ein Rückgang der Tarsuslänge beobachtet wurde, fand sich keine Veränderung der Körpermasse. Die Zunahme der Flügel- und Schwanzlänge könnte mit der Veränderung der trophischen Nische als Anpassung an das rückläufige Wasservolumen der Flüsse zusammenhängen, das im Untersuchungszeitraum auftrat. Andere Arbeiten zeigen, dass sich die Nahrung der Wasserramsel mit der Stärke des Wasserstroms ändert, und der Wasserstrom ging im Untersuchungsgebiet als Folge der Klimaerwärmung zurück.

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