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Research

Variation in wing morphology is related to breeding environment in a high-elevation specialist bird

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The morphology of bird wings is subject to a variety of selective pressures, including migration, predation, habitat structure and sexual selection. Variation in wing morphology also occurs at the intraspecific and intrapopulation level, and can be related to sex, age, migration strategy and environmental factors. The relationship between environment and intraspecific variation in wing morphology is still poorly understood. In this work, we studied the relationship between wing morphology and breeding environment in a high-elevation specialist bird, the water pipit *Anthus spinoletta*. We calculated wing isometric size, pointedness and convexity of 84 birds mist-netted at breeding sites in year 2021 in the European Alps. We then searched for associations between these traits and potentially relevant breeding site characteristics (vegetation structure, elevation, latitude). For all wing traits, sex and one or more environmental factors best explained the variation, with environmental factors explaining between 3 and 8% of the variation. Wing size was negatively related to tree cover and wing convexity was negatively related to bush cover. Elevation contributed to explain variation in wing pointedness, but the direction of its effect was unclear. The negative relationship between wing size and tree cover could be due to intraspecific competition, i.e. to the relegation of smaller winged low-quality individuals in marginal grassland areas. Higher wing convexity could improve predator escape ability in areas with scarce protecting vegetation, with possible effects on habitat choice. These findings represent one of the few demonstrated cases of wing morphology–environment relationships at the intraspecific level.

Keywords: *Anthus spinoletta*, bird morphology, elevational gradient, water pipit, wing convexity, wing pointedness



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Introduction

Locomotor apparatus of organisms are subject to a variety of selective pressures. The morphology of birds' wings has been the object of several studies, often based on interspecific comparisons, carried out to identify selective pressures such as migration (Lockwood et al. 1998, Piersma et al. 2005), predation (Marchetti et al. 1995, Burns and Ydenberg 2002), habitat structure (Lindhe Norberg 2002, Kaboli et al. 2007, Desrochers 2010) and sexual selection (Hedenström and Møller 1992). Migration strongly influences wing morphology, selecting for longer and more pointed wings that allow a more efficient flight, reducing energy costs of long migratory movements (Lockwood et al. 1998). Coevolution of predators and preys contributes to shape bird wings due to the advantages in terms of flight speed/manoeuvrability stemming from specific wing characteristics (Marchetti et al. 1995, Swaddle and Lockwood 2003). Birds living in dense vegetation often show more rounded wings than open-habitat species, because of the need of higher flight manoeuvrability (Lindhe Norberg 2002, Desrochers 2010). Sexual selection on wing morphology is especially relevant in species performing song flights, as demonstrated by comparing wing traits of species performing and not performing these flight displays (Hedenström and Møller 1992).

Variation in wing morphology also occurs at the intraspecific level, across as well as within populations (Berthold 1996, Arizaga et al. 2006, Rolshausen et al. 2009, Baldwin et al. 2010, Delingat et al. 2011, Neto et al. 2013). Such variation is often linked with sexual dimorphism (Szekely et al. 2007), but can also be related to age (Alatalo et al. 1984, Figuerola and Gutiérrez 2000, García et al. 2021), to within-population differences in migration strategy (Rolshausen et al. 2009) or to environmental factors such as vegetation structure (Vanhooydonck et al. 2009, Saino et al. 2017). The relationship between intraspecific variation in wing morphology and environment has been scarcely investigated and is therefore still poorly understood. Saino et al. (2017) found support for different habitat choice by individuals with different wing morphology in barn swallows *Hirundo rustica*, probably due to advantages provided by specific morphological characteristics in different contexts (in this case, more rounded wings in denser vegetation). Covariation between wing morphology and environmental factors can also arise from different habitat use, when specific wing morphology traits (e.g. wing size) are related to individual quality and thus, fitness (Méró et al. 2020). While studies considering habitat characteristics like vegetation/land cover in relation to wing morphology are very scarce, the influence of elevation has been more intensively investigated, mostly in relation to wing length (Laiolo and Rolando 2001, Lu et al. 2009, Wilson et al. 2010, Boyce et al. 2019, Sander and Chamberlain 2020). These studies have given partly contrasting results, often indicating the lack of elevational patterns, or a positive wing length–elevation relationship in different studies/species. Such cases of positive relationships could be interpreted as a need for a more efficient flight in conditions of lower air pressure and

higher hypoxia risk associated with higher elevations (Sander and Chamberlain 2020). While these studies provided extremely valuable information, the lack of consideration of other environmental factors in addition to elevation, such as vegetation or land cover, complicates interpretation. In fact, wing morphology variation along elevational gradients could be also partly due to variations in vegetation characteristics occurring along the same gradient. The latter is a pattern regularly observed through mountain chains worldwide (Gentry 1988, Ozenda 1988, Luna-Vega et al. 2001, Zhu et al. 2005). In addition, while most authors considered wing size, variation in wing shape across elevational gradients is still almost unexplored (but see García et al. 2021). Therefore, the role of elevation in shaping wing morphology is still unclear, and studies along elevational gradients considering both elevation and other environmental factors are needed.

In this study, we investigated the relationship between intraspecific variation in wing morphology and environmental factors in a high-elevation specialist bird, the water pipit *Anthus spinoletta*, across a wide environmental and elevational gradient within a large area in the European Alps. Water pipit is a small bird (ca 20 g) breeding in mountain ranges of south and central Europe, Middle East and central Asia, with the easternmost breeding areas in northern and central China (Tyler 2019). This species breeds in mountainous open areas, such as alpine grasslands and pastures, often scattered with rocks, bushes or trees, and usually performs elevational or short-distance migration movements, overwintering in lowland areas (Bricchetti and Fracasso 2007, Spina and Volponi 2008, Tyler 2019). Migration strategies of water pipits breeding in our study area and, more generally, in the Italian Alps are poorly known. They may overwinter in Alpine valley floors as well as in the lowlands near the mountain chain, and/or along the Mediterranean coasts (Spina and Volponi 2008). Male water pipits perform song flights and have longer wings than females (Demongin 2016).

We investigated the wing morphology–environment relationship in the water pipit by considering vegetation characteristics, elevation and latitude of breeding sites, while accounting for birds' sex and age. As wing morphology traits, we considered wing size, pointedness and convexity. Wing pointedness describes the shift in the position of the wingtip feather towards the wing leading edge; higher pointedness allows a more energy efficient flight, while more rounded wings increase flight manoeuvrability (Lockwood et al. 1998). Wing convexity measures the decrease in the acuteness of the wingtip, and higher convexity is associated to higher thrust and faster take-off, while more concave wings have lower wing weight and inertia (Lockwood et al. 1998). We expected to find associations between wing morphology traits and both land cover and elevation, as a consequence of differences in breeding habitat selection by individuals with partly different wing morphology. This scenario is especially likely in our study system, because the steep elevational and environmental gradients of mountain areas result in strongly different conditions within short distances, thus potential breeding sites with very different characteristics can

be explored with reduced displacement costs by prospecting individuals. More specifically, we expected: 1) a negative relationship between wing pointedness and bush/tree cover, as birds with more rounded wings may be advantaged in denser vegetation; 2) a negative relationship between wing size and bush/tree cover, as wing size is often considered a proxy of individual quality in birds (Saino et al. 2017, MÉRŐ et al. 2020), and grassland edges with higher occurrence of bushes and trees are likely to be occupied by poorly competitive individuals. High bush/tree cover is indeed detrimental for this grassland species (Melendez and Laiolo 2014, Ceresa et al. 2020). We also expected 3) a positive relationship between elevation and both wing size and pointedness, as a more energetically efficient flight should be beneficial in conditions of lower air pressure and higher hypoxia risk (Altshuler and Dudley 2006, Scott 2011). Although the latitudinal range of our study area is relatively reduced (approx. 150 km), we also considered this factor because we could not exclude variation in migration distances across this range. We expected 4) no or a very weak influence of latitude, given this limited range and the likely high relevance of elevational migration in our system.

Material and methods

Data collection

Fieldwork took place in the central-eastern Italian Alps, in the Trentino-South Tyrol region, which covers an area of approx. 13 600 km² ranging from the peripheral massifs of the Pre-Alps in the south to the main Alpine watershed in the north. Within this region, in year 2021, we captured water pipits with mist-nets and spring traps at 10 sampling areas (Fig. 1), representing nearly the entire elevational and environmental gradient occupied by the species in the region. Sampling areas included semi-open, ecotonal zones near the treeline and wide treeless alpine grasslands, continuous or interspersed with rocks or scree. Within each sampling area, we captured birds at several different sites, resulting in 55 different capture sites spanning from 1590 up to 2530 m a.s.l. Water pipits also occupy areas at higher elevations, but within the study region the occurrence probability of this species rapidly decreases above 2500 m a.s.l. (Chamberlain et al. 2016, Ceresa et al. 2020); therefore, the elevational gradient we considered is representative of

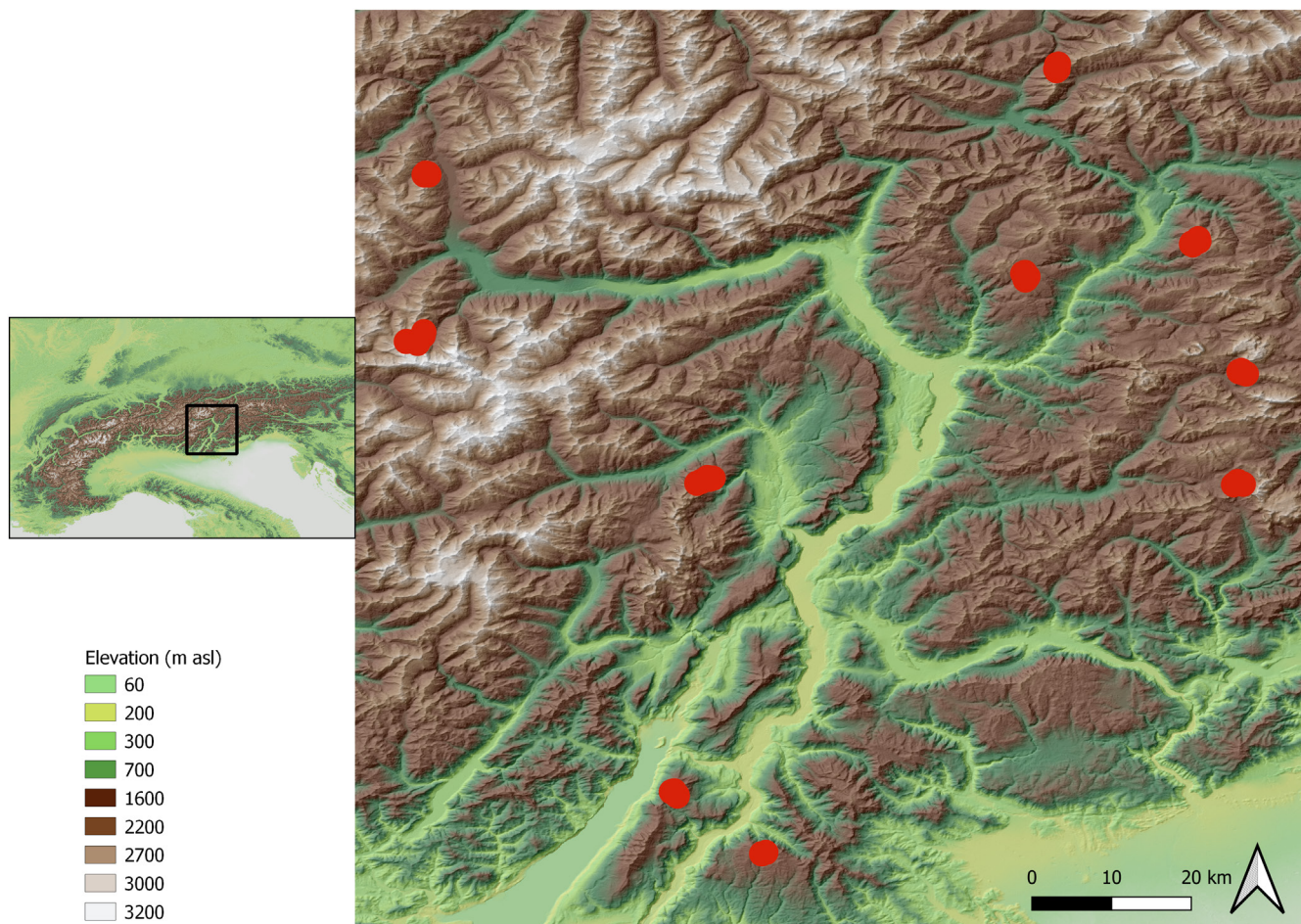


Figure 1. Location of the sampling sites (red dots) in the central-eastern Italian Alps; the inset shows the location of the study area within the Alpine region.

the environmental conditions experienced by the local water pipit breeding population. We performed sampling during the water pipit's breeding season, from the end of May to mid-July. This timing allowed excluding the migration periods of this species (Spina and Volponi 2008). We used recorded male songs to improve capture probability (otherwise extremely low), which resulted in a majority of males within our sample ($n=84$, of which 78 males and 6 females). At each capture site (mist-net transect or set of spring traps) we also recorded information about vegetation characteristics within a 100 m-radius, including the percentage cover of tree canopy (vegetation higher than 2 m) and bushes (woody vegetation lower than 2 m). Percentage cover of vegetation categories was visually estimated in the field to the nearest 5%; variables estimated to cover less than 5% of the 100 m-radius plot were assigned a 1% cover value.

Each bird was first marked with a metal ring of the Italian ringing scheme, in order to avoid repeated samplings. Age and sex were attributed based on criteria from Svensson (1992) and Demongin (2016). For this species and season, birds can be determined to be 1st year birds, 2nd year birds or older than 2 years, although we only captured 2nd year birds or older individuals. Details about the number of measured birds per site, including sex and ages, are provided in the Supporting information. Length of 9 primary wing feathers (all excepted the outermost, vestigial one) were measured from feather tip to the point where it enters skin by means of a metal ruler (± 0.5 mm). We measured primary feathers lengths instead of distances among feather tips because it allows a lower measurement error (feathers are far larger than distances among tips) and better repeatability (Swaddle and Witter 1997, Lockwood et al. 1998). Measurements were taken following the same protocol by two of the authors, who are expert bird ringers. Besides adopting a highly repeatable measure, we compared measurements of a primary feather (P8) taken by both ringers from the same individuals of species with wing size very similar to water pipit. This comparison showed the lack of measurement differences between ringers (details in the Supporting information).

When studying wing morphology, it is crucial to distinguish between wing size and shape, because shape measures that are not completely independent from individual size imply serious interpretation problems (Lockwood et al. 1998). Principal components analysis (PCA) has been used in several morphological studies to try separating size and shape, interpreting the first component as a measure of size and the subsequent components as shape indexes (Jolicoeur and Mosimann 1960). However, PCA does not effectively disentangle shape and size, as the first component also incorporates shape, and the subsequent ones are not independent from size (Mosimann 1970, Humphries et al. 1981, Lockwood et al. 1998). Other approaches have been proposed to remove allometric effects from body measurements before analysing shape traits, such as the ratio methods (Mosimann and James 1979) or a scaling procedure based on allometric models (Leonart et al. 2000). However, ratio

methods have been found to be ineffective and potentially misleading in removing size effects (Packard and Boardman 1988, Leonart et al. 2000), and scaling based on allometric models, despite its effectiveness, can become complex when allometric parameters vary within the sample, e.g. in case of strong sexual dimorphism like in the water pipit (Leonart et al. 2000). Therefore, we used size-constrained component analysis (SCCA; Lockwood et al. 1998), a widely adopted approach allowing to effectively separate wing size from wing shape measures. For each individual, we obtained three wing morphology indices from primary feathers lengths: the first component (C1) represents isometric wing size (i.e. wing size independent from its shape), the second one (C2) is a wing pointedness index and the third one (C3) represents wing convexity. SCCA components were calculated by applying the formula reported in Lockwood et al. (1998). C2 increases with decreasing wing pointedness, therefore it should be interpreted as a roundness index. The ranges of variation of these three morphological traits within our sample are represented in Fig. 2, and basic statistics for primary feather measurements are provided in the Supporting information.

Besides adopting the approach that best suited our aims (i.e. SCCA), we also used PCA, in order to check the consistency of our results across different methods and to allow comparisons with other studies using PCA, which is also often used in morphological studies. We reduced primary feathers lengths to principal components using function 'prcomp' of package stats in program R ver. 4.1.1 (<www.r-project.org>). Based on component loadings (Supporting information), we interpreted components PC1, PC2 and PC3 as proxies for wing size, pointedness and convexity, respectively.

Statistical analysis

We investigated the relationship between wing morphology and environmental factors by means of multiple linear regression, using the 'lm' function of package stats in program R ver. 4.1.1 (<www.r-project.org>). We considered, in turn, the SCCA component describing isometric wing size (C1), wing pointedness (C2) and wing convexity (C3) as response variable, and elevation, latitude, tree canopy cover, bush cover, age and sex as predictors. Continuous predictors were standardized by means of the scale function. For each wing morphology index, we ranked all possible linear models according to the respective value of the Akaike information criterion corrected for small sample size (AICc), using the ' dredge ' function of R package MuMIn (Bartoń 2020). Prior to model selection, we assessed collinearity among covariates by means of the variance inflation factor (VIF), using the 'vif' function of R package car (Fox and Weisberg 2019). The highest VIF was 1.7, therefore we did not consider collinearity (Zuur et al. 2010). To estimate the effect of predictors on the response variable, after removing the uninformative parameters (Arnold 2010) we performed a full model averaging across all models with $\Delta AICc < 2$ (Burnham and Anderson 1998).

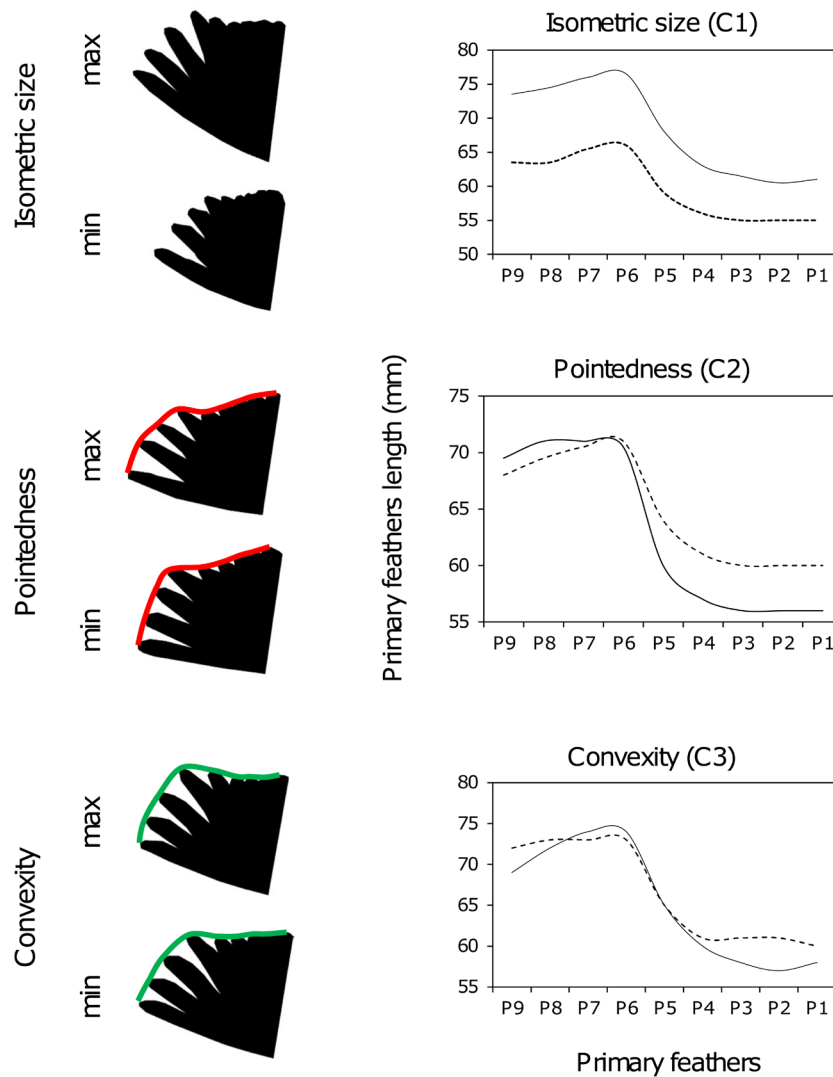


Figure 2. Graphical representation of the ranges of isometric wing size, wing pointedness and wing convexity within the considered sample of 84 water pipits. Wingtips (on the left) and primary feathers lengths (on the right) are depicted for those individuals respectively with larger, more pointed and more convex wings (solid lines in the graphs) and with smaller, more rounded and more concave wings (dashed lines in the graphs) within our sample. Primary feathers are numbered ascendingly and excluding the outermost, vestigial one (P10). Wingtip figures were drawn based on photos of wings taken during fieldwork.

We checked for spatial autocorrelation by calculating Moran's I for model residuals in ArcGis ver. 10.8, considering several different threshold distances (~1, 10 and 40 km) to look for possible clustering of residuals at different spatial scales. In order to gain further insight about the morphology–environment relationship, we used variation partitioning to assess the proportion of variability in wing morphology explained only by environmental factors. We considered only those variables included in the most supported models, i.e. informative parameters, and we performed the analysis using the function *varpart* in R package *vegan* (Oksanen et al. 2020).

We carried out the additional PCA-based analysis by repeating the same model selection and model averaging procedures described above, using the three principal components obtained by PCA instead of SCCA components.

Results

For all wing morphology traits, the most supported models (i.e. with $\Delta AICc < 2$) included sex and one or more environmental variables: tree cover for wing size; elevation and tree cover for wing pointedness; bush and tree cover for wing convexity (Table 1). Some of these predictors showed a clear effect according to multi model averaging, as 95% confidence intervals of averaged β did not include 0 (Table 2, Fig. 3): isometric wing size was negatively related to tree cover ($\beta = -0.008$; CI 95% -0.015 to -0.001) and wing convexity was negatively related to bush cover ($\beta = -0.045$; CI 95% -0.086 to -0.005). Females showed smaller and more rounded wings (Table 2). Model residuals were normally distributed (wing size and pointedness) or approached normality at visual exploration

Table 1. Best linear regression models ($\Delta\text{AICc} < 2$) for wing morphology according to the corrected Akaike information criterion (AICc), and full model for each response variable (in italics). Trees: % cover of tree canopy within a 100 m-radius around bird capture site; bushes: % cover of bushes within a 100 m-radius around bird capture site.

Response variable	Model	ΔAICc
Wing size (C1)	Sex + trees	0.00
	<i>Elevation + latitude + sex + age + bushes + trees</i>	7.71
Wing pointedness (C2)	Elevation + sex + trees	0.00
	Elevation + sex	0.71
	Sex + trees	1.43
	<i>Elevation + latitude + sex + age + bushes + trees</i>	6.99
Wing convexity (C3)	Bushes + sex + trees	0.00
	Bushes + trees	0.63
	Bushes + sex	1.08
	<i>Elevation + latitude + sex + age + bushes + trees</i>	8.71

(wing convexity). We found no evidence for spatial autocorrelation in model residuals (Moran's I range: -0.181 to -0.067 ; p-values range: 0.26 – 0.71). Based on the adjusted determination coefficient (R^2_{adj}), best models explained 39% of variability in wing size, 13% in wing pointedness and 10% in wing convexity. According to variation partitioning, environmental factors (vegetation/elevation) overall explained 3% of variability in wing size and 8% in both wing pointedness and convexity.

Two especially high values of tree cover (Fig. 3) may have disproportionately influenced the results about isometric wing size. Therefore, we re-fitted our models for C1 by including trees in ways that eliminated or reduced the effect of the two highest values. First, we replaced tree cover with tree presence/absence (included as a binary factor); this implies a large loss of information about tree cover, but in spite of this, this factor resulted to be an informative predictor according to model selection as it was included in the best model, although its negative effect was weaker than percentage tree cover ($\beta = -0.012$, $\text{SE} = 0.007$; CI 85% did not include 0). As a further check, we log-transformed tree cover, which strongly reduced the difference between most data and the highest values, and we replaced tree cover with the transformed variable in C1 model selection; log-transformed tree cover was an informative predictor as it was included in the best model, and showed an even stronger negative effect than using the untransformed values ($\beta = -0.021$, $\text{SE} = 0.010$; CI 95% did not include 0). All these results indicated the lack of disproportionate effects of the two aforementioned data on our results.

Comparing the aforementioned SCCA-based results with the additional PCA-based analysis (results in Supporting information), we obtained very similar results between PC1 and C1 and between PC2 and C2, and different results between PC3 and C3, possibly because the effect of allometry was stronger on PC3 (the component explaining the lower amount of morphological variation, Supporting information).

Discussion

Our findings represent one of the very few demonstrated cases of relationship between intraspecific wing morphology variation and habitat structure (Vanhooydonck et al. 2009, Saino et al. 2017, Méréo et al. 2020). While we expected the occurrence of such a general effect of habitat structure, some of the more specific expectations we initially formulated were not confirmed (see the following sections). Overall, vegetation structure was clearly more influent than topographic/geographic factors, as tree or bush cover were included in the best models of all morphological traits. Smaller wings in areas with higher tree cover is consistent with our expectations: these marginal areas are likely occupied by low quality individuals, and wing size can be interpreted as a proxy of individual quality in passerine birds (Nowakowski 2000, Forstmeier et al. 2001, Méréo et al. 2020). These small-winged individuals are probably excluded from more suitable breeding sites by more competitive conspecifics. While we cannot completely exclude possible advantages of smaller wings in

Table 2. Effects of predictors on wing morphology according to multi model averaging on the best models (Table 1). Trees: % cover of tree canopy within a 100 m-radius around bird capture site; bushes: % cover of bushes within a 100 m-radius around bird capture site. The wing pointedness index (C2) is inversely related to pointedness.

Response variable	Predictor	Effect (SE)	-95% CI	+95% CI
Wing size (C1)	Sex (female)	-0.101 (0.004)	-0.108	-0.093
	Trees	-0.008 (0.004)	-0.015	-0.001
Wing pointedness (C2)	Elevation	0.018 (0.014)	-0.010	0.045
	Sex (female)	0.103 (0.044)	0.017	0.189
	Trees	-0.014 (0.013)	-0.039	0.012
Wing convexity (C3)	Sex (female)	-0.092 (0.091)	-0.270	0.086
	Bushes	-0.045 (0.021)	-0.086	-0.005
	Trees	0.028 (0.024)	-0.019	0.076

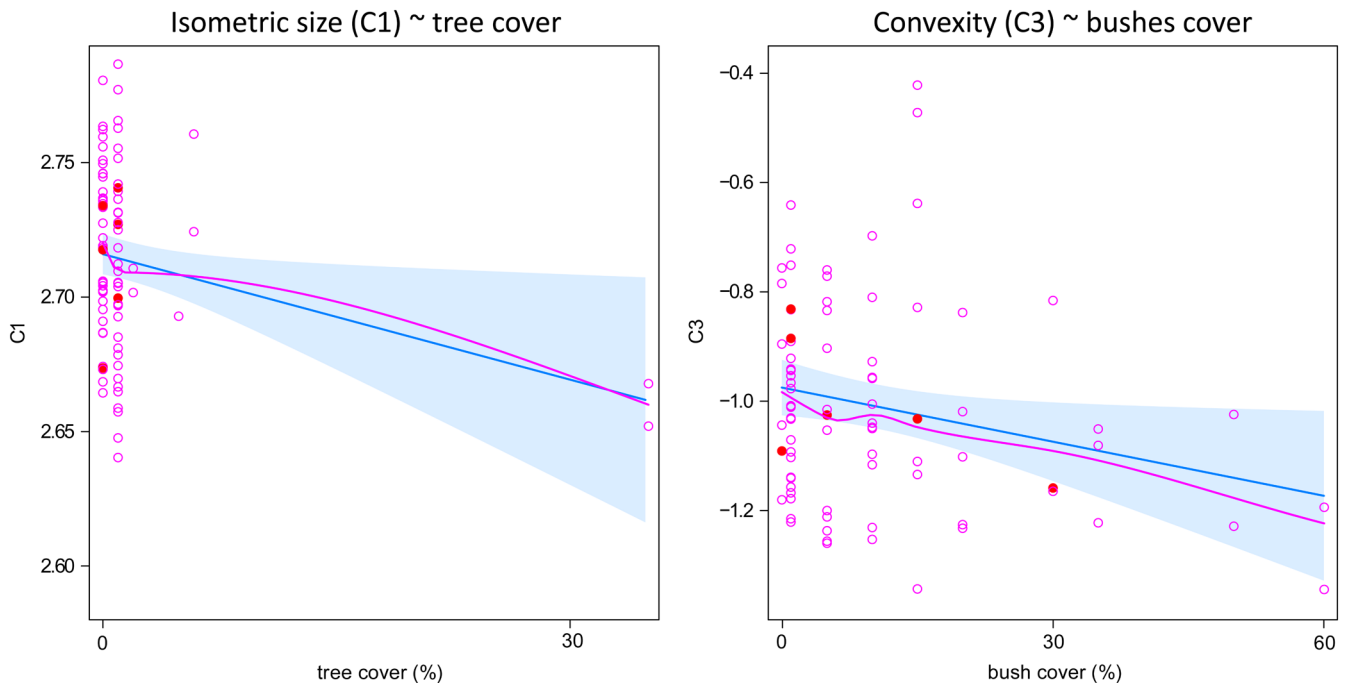


Figure 3. Effects of breeding site vegetation cover on water pipit wing morphology. 95% CI are shown in light blue. Dots represents partial residuals (pink: males, red: females) and the pink line is a smoothed spline interpolating partial residuals.

denser vegetation in terms of better flight manoeuvrability, we would rather expect such advantages to be connected to wing shape (i.e. more rounded wings) rather than to wing size (Lockwood et al. 1998, Desrochers 2010, Saino et al. 2017). In addition, this alternative explanation would imply niche segregation and even genetic divergence among individuals with different wing morphology, a scenario that seems highly unlikely in our study system. Tree cover is included also in the best models of both wing shape indices (Table 1), but in these cases the direction of its effect is unclear (95% confidence intervals include 0). Even if tree cover was an informative parameter in the models (cf. Arnold 2010), and thus it is likely to be actually related to wing shape, its effect was probably weak and perhaps our sample size was not large enough to detect a stronger effect. Differently from tree cover, bush cover showed a clear effect on wing shape, being negatively associated to wing convexity.

More convex wings allow a faster take-off and at a steeper angle, which could represent an advantage in areas with scarce or no bushy vegetation to protect from predators. The initial take-off is indeed crucial when escaping from predators (Kenward 1978), and a steeper take-off, rather than faster horizontal acceleration, is likely advantageous in absence of nearby protective vegetation cover to hide (Kullberg and Lafrenz 2007). In our study area, water pipits face a variety of both aerial and terrestrial predators (e.g. Eurasian sparrowhawk *Accipiter nisus*, Eurasian hobby *Falco subbuteo*, red fox *Vulpes vulpes*, stoat *Mustela erminea*), and predation risk can affect habitat choice (Thomson et al. 2006), therefore different escape abilities connected to different wing shapes could affect habitat selection by breeding water pipits. A detailed

investigation of the escape strategies from different predator species in this bird species would be needed to verify this hypothesis (Burns and Ydenberg 2002). Previous studies on passerine birds have alternatively assessed the occurrence (Mérő et al. 2020) or the lack (García et al. 2021) of association between variation in wing morphology and vegetation structure. While the number of studies about this issue is still reduced to raise any conclusions, our results and the previous findings suggest that such association is probably species- (and possibly context-) dependent.

Wing size was not associated with elevation in our sample (differently from the expectation), and for wing pointedness the relationship with elevation remained unclear. Elevation is indeed likely to be actually related to wing pointedness, but probably weakly, thus requiring a larger sample size to result in a clearer effect. No or very weak association between wing morphology and elevation in the water pipit may be explained by the clear specialization for high-elevation in this species. All individuals may indeed be adequately adapted to flight conditions at high elevations, and possible small advantages represented by longer or more pointed wings may be overridden by several more relevant factors during breeding habitat selection. Alternatively, the pattern we observed could be common among birds, as suggested also by some previous studies (Boyce et al. 2019, García et al. 2021). Further studies considering elevation in combination with other potentially relevant environmental factors are needed to better clarify the relationship between intraspecific variation in bird wing morphology and elevation.

Inclusion of sex in our analysis was motivated by the need to account for the expected sexual dimorphism in wing

morphology. In fact, our data are not suited to describe sexual dimorphism in detail, given the low number of females in our sample. The observed patterns anyway deserve a short comment. Besides the well-known difference in wing size (Demongin 2016), our results also suggest possible differences in wing shape, especially in wing pointedness. These differences may be due to sexual selection connected to males' song flight (Hedenström and Møller 1992). Longer and more pointed wings improve flight efficiency, which is a relevant advantage especially when performing frequent song flights in the challenging conditions of high mountain areas (thin air, harsh weather). Although the effect is not clear (Table 2), probably due to the low number of females, our results suggest more convex wings in males. This could represent a compensation for a reduced flight manoeuvrability caused by high pointedness, as suggested by Minias et al. (2013) for the common snipe *Gallinago gallinago*. Common snipe males also perform song flights and have more pointed and convex wings than females. Different evolutionary pressures on wing morphology act in combination, potentially also in an antagonistic way (Lockwood et al. 1998), and a loss of manoeuvrability due to song flight-related high pointedness possibly needs to be compensated to maintain sufficient predator escape abilities.

Environmental characteristics of the breeding sites overall explained a relatively small part of variability in wing morphology traits (3–8%). This is not surprising, as only part of the inter-individual morphological differentiation is potentially connected to advantages/disadvantages at different breeding environments, or to mechanisms influencing habitat choice, such as intraspecific competition (e.g. part of the variability within our sample was due to sexual dimorphism). In addition, a variety of factors influence habitat choice in birds, and factors likely unrelated to morphology (e.g. food abundance, predator density) may partly or completely override possible context-specific advantages connected to wing shapes and sizes. The proportion of unexplained data variability remained relatively high even considering also sexual dimorphism in addition to environmental factors. A possible source of unexplained variation in wing morphology may be the occurrence of within-population differences in migration strategy (Rolshausen et al. 2009). In our study area water pipits may be partly elevational and partly short-distance migrants, and the latter may overwinter at varying distances from breeding sites. This is a very likely scenario, as valley floors within the study area do host wintering water pipits, but apparently with much lower numbers when compared to the abundant local breeding population. Our results suggest that possible differences in migration strategy should be unrelated to the latitudinal gradient, or too weakly related, to determine morphological differences, given the lack of latitudinal effects on wing morphology (consistently with our expectations).

Vagrant/prospecting individuals with no ties to a specific breeding site, if occurring in our sample, could present a possible source of bias in the analysis. However, all captured individuals were sexually mature (2nd year or older), and all showed

well developed cloacal protuberances or incubation patches. In addition, males were captured when they aggressively reacted to recorded songs, and they were often observed during persistent song flight both before and after the capture. This strongly suggests that all captured birds were breeding individuals, and the inclusion of vagrants was extremely unlikely.

Comparing SCCA- and PCA-based analyses, the similar results using C1/PC1 and C2/PC2 indicate the strong robustness of our results about wing size and pointedness, because they did not change significantly using two different approaches; this suggests that, while PCA cannot fully separate size and shape (Humphries et al. 1981, Lockwood et al. 1998), in this case the influence of wing shape on PC1 and of wing size on PC2 was weak. The difference between C3 and PC3 results may be due to a stronger effect of allometry on this PCA component. PC3 seemed indeed a less adequate index of convexity than C3, as it carried virtually no information about a large part of the wing (see Supporting information, and the graphical representation of convexity in Lockwood et al. 1998 for a comparison). Therefore, our results obtained using C3 are very likely more reliable than PC3-based models.

In conclusion, we assessed the association between intraspecific variation in wing morphology and some environmental characteristics of breeding sites in a high-elevation specialist bird. As a possible mechanism underlying the observed associations, we proposed habitat choice of water pipits to be influenced by intraspecific competition (wing size – tree cover association) and predation escape strategies (wing convexity – bush cover association). Elevation contributed to explain variation in wing shape, but the direction of the effect of this factor was unclear, possibly because the actual effect is very weak. This could be due to the specialization for high-elevation environments in the water pipit, or could represent patterns where other factors override the effect of elevation. Further studies along both elevational and environmental gradients are needed to better clarify the elevation–wing morphology relationship.

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Data are available from the Figshare Digital Repository: <https://figshare.com/articles/dataset/Data_Variation_in_wing_morphology_is_related_to_breeding_environment_in_a_high-elevation_specialist_bird/20750452> (Ceresa et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Alatalo, R. V., Gustafsson, L. and Lundberg, A. 1984. Why do young passerine birds have shorter wings than older birds? – *Ibis* 126: 410–415.
- Altshuler, D. L. and Dudley, R. 2006. The physiology and biomechanics of avian flight at high altitude. – *Integr. Comp. Biol.* 46: 62–71.
- Arizaga, J., Campos, F. and Alonso, D. 2006. Variations in wing morphology among subspecies might reflect different migration distances in bluethroat. – *Ornis Fenn.* 83: 162.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. – *J. Wildl. Manage.* 74: 1175–1178.
- Baldwin, M. W., Winkler, H., Organ, C. L. and Helm, B. 2010. Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats *Saxicola torquata*. – *J. Evol. Biol.* 23: 1050–1063.
- Bartoń, K. 2020. MuMIn: multi-model inference. – <<https://cran.r-project.org/web/packages/MuMIn/index.html>>.
- Berthold, P. 1996. Control of bird migration. – Springer Science and Business Media.
- Boyce, A. J., Shakya, S., Sheldon, F. H., Moyle, R. G. and Martin, T. E. 2019. Biotic interactions are the dominant drivers of phylogenetic and functional structure in bird communities along a tropical elevational gradient. – *Auk* 136: ukz054.
- Brichetti, P. and Fracasso, G. 2007. *Ornitologia italiana*, vol. 4. Apodidae–Prunellidae. – Oasi Alberto Perdisa Editore.
- Burnham, K. P. and Anderson, D. R. 1998. Practical use of the information–theoretic approach. – In: *Model selection and inference*. Springer, pp. 75–117.
- Burns, J. G. and Ydenberg, R. C. 2002. The effects of wing loading and gender on the escape flights of least sandpipers *Calidris minutilla* and western sandpipers *Calidris mauri*. – *Behav. Ecol. Sociobiol.* 52: 128–136.
- Ceresa, F., Brambilla, M., Monrós, J. S., Rizzolli, F. and Kranebitter, P. 2020. Within-season movements of Alpine songbird distributions are driven by fine-scale environmental characteristics. – *Sci. Rep.* 10: 5747.
- Ceresa, F., Vitulano, S., Pes, M., Tomasi, L., Brambilla, M., Kvist, L., Pedrini, P., Anderle, M., Hilpold, A. and Kranebitter, P. 2022. Data from: Variation in wing morphology is related to breeding environment in a high-elevation specialist bird. – Figshare Digital Repository, <https://figshare.com/articles/dataset/Data_Variation_in_wing_morphology_is_related_to_breeding_environment_in_a_high-elevation_specialist_bird/20750452>.
- Chamberlain, D., Brambilla, M., Caprio, E., Pedrini, P. and Rolando, A. 2016. Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions. – *Oecologia* 181: 1139–1150.
- Delingat, J., Hobson, K. A., Dierschke, V., Schmaljohann, H. and Bairlein, F. 2011. Morphometrics and stable isotopes differentiate populations of northern wheatears *Oenanthe oenanthe*. – *J. Ornithol.* 152: 383–395.
- Demongin, L. 2016. Identification guide to birds in the hand. – Beauregard-Vendon.
- Desrochers, A. 2010. Morphological response of songbirds to 100 years of landscape change in North America. – *Ecology* 91: 1577–1582.
- Figuerola, J. and Gutiérrez, R. 2000. Why do juvenile moustached warblers have shorter wings? – *Ornis Fenn.* 77: 183–187.
- Forstmeier, W., Bourski, O. V. and Leisler, B. 2001. Habitat choice in *Phylloscopus warblers*: the role of morphology, phylogeny and competition. – *Oecologia* 128: 566–576.
- Fox, J. and Weisberg, S. 2019. An R companion to applied regression, 3rd edn. – SAGE Publications.
- García, J., Arizaga, J., Rodríguez, J. I., Alonso, D. and Suárez-Seoane, S. 2021. Morphological differentiation in a migratory bird across geographic gradients in mountains of southern Europe. – *J. Biogeogr.* 48: 2828–2838.
- Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. – *Ann. Mo. Bot. Gard.* 75: 1–34.
- Hedenström, A. and Møller, A. P. 1992. Morphological adaptations to song flight in passerine birds: a comparative study. – *Proc. R. Soc. B* 247: 183–187.
- Humphries, J. M., Bookstein, F. L., Chernoff, B., Smith, G. R., Elder, R. L. and Poss, S. G. 1981. Multivariate discrimination by shape in relation to size. – *Syst. Biol.* 30: 291–308.
- Jolicoeur, P. and Mosimann, J. E. 1960. Size and shape variation in the painted turtle. A principal component analysis. – *Growth* 24: 339–354.

- Kaboli, M., Aliabadian, M., Guillaumet, A., Roselaar, C. S. and Prodon, R. 2007. Ecomorphology of the wheatears (genus *Oenanthe*). – *Ibis* 149: 792–805.
- Kenward, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. – *J. Anim. Ecol.* 47: 449–460.
- Kullberg, C. and Lafrenz, M. 2007. Escape take-off strategies in birds: the significance of protective cover. – *Behav. Ecol. Sociobiol.* 61: 1555–1560.
- Laiolo, P. and Rolando, A. 2001. Ecogeographic correlates of morphometric variation in the red-billed chough *Pyrrhocorax pyrrhocorax* and the alpine chough *Pyrrhocorax graculus*. – *Ibis* 143: 602–616.
- Lindhe Norberg, U. M. 2002. Structure, form and function of flight in engineering and the living world. – *J. Morphol.* 252: 52–81.
- Leonart, J., Salat, J. and Torres, G. J. 2000. Removing allometric effects of body size in morphological analysis. – *J. Theor. Biol.* 205: 85–93.
- Lockwood, R., Swaddle, J. P. and Rayner, J. M. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. – *J. Avian Biol.* 29: 273–292.
- Lu, X., Ke, D. H., Zeng, X. H. and Yu, T. L. 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: response to more stressful environments. – *J. Arid Environ.* 73: 1103–1108.
- Luna-Vega, I., Morrone, J. J., Ayala, O. A. and Organista, D. E. 2001. Biogeographical affinities among Neotropical cloud forests. – *Plant Syst. Evol.* 228: 229–239.
- Marchetti, K., Price, T. and Richman, A. 1995. Correlates of wing morphology with foraging behaviour and migration distance in the genus *Phylloscopus*. – *J. Avian Biol.* 26: 177–181.
- Melendez, L. and Laiolo, P. 2014. The role of climate in constraining the elevational range of the water pipit *Anthus spinoletta* in an alpine environment. – *Ibis* 156: 276–287.
- Mérő, T. O., Žuljević, A., Varga, K. and Lengyel, S. 2020. Wing size-related habitat choice of great reed warbler females: the role of habitat quality and management. – *Avian Conserv. Ecol.* 15: 22.
- Minias, P., Kaczmarek, K., Włodarczyk, R. and Janiszewski, T. 2013. Wing shape influences stopover strategies in a migratory shorebird, the common snipe. – *Condor* 115: 535–542.
- Mosimann, J. E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. – *J. Am. Stat. Assoc.* 65: 930–945.
- Mosimann, J. E. and James, F. C. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. – *Evolution* 33: 444–459.
- Neto, J. M., Gordinho, L., Belda, E. J., Marín, M., Monrós, J. S., Fearon, P. and Crates, R. 2013. Phenotypic divergence among west European populations of reed bunting *Emberiza schoeniclus*: the effects of migratory and foraging behaviours. – *PLoS One* 8: e63248.
- Nowakowski, J. J. 2000. Long-term variability of wing length in a population of the reed warbler *Acrocephalus scirpaceus*. – *Acta Ornithol.* 35: 173–182.
- Oksanen et al. 2020. vegan: community ecology package. – <https://cran.r-project.org/web/packages/vegan/index.html>.
- Ozenda, P. 1988. Die Vegetation der Alpen im europäischen Gebirgsraum. – Fischer.
- Packard, G. C. and Boardman, T. J. 1988. The misuse of ratios, indices and percentages in ecophysiological research. – *Physiol. Zool.* 61: 1–9.
- Piersma, T., Pérez-Tris, J., Mouritsen, H., Bauchinger, U. L. F. and Bairlein, F. 2005. Is there a ‘migratory syndrome’ common to all migrant birds? – *Ann. N. Y. Acad. Sci.* 1046: 282–293.
- Rolshausen, G., Segelbacher, G., Hobson, K. A. and Schaefer, H. M. 2009. Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. – *Curr. Biol.* 19: 2097–2101.
- Saino, N., Ambrosini, R., Caprioli, M., Liechti, F., Romano, A., Rubolini, D. and Scandolaro, C. 2017. Wing morphology, winter ecology and fecundity selection: evidence for sex-dependence in barn swallows *Hirundo rustica*. – *Oecologia* 184: 799–812.
- Sander, M. M. and Chamberlain, D. 2020. Evidence for intraspecific phenotypic variation in songbirds along elevation gradients in central Europe. – *Ibis* 162: 1355–1362.
- Scott, G. R. 2011. Elevated performance: the unique physiology of birds that fly at high altitudes. – *J. Exp. Biol.* 214: 2455–2462.
- Spina, F. and Volponi, S. 2008. Atlante della Migrazione degli Uccelli in Italia 2. Passeriformi [Italian bird migration atlas]. – Ministero dell’Ambiente e della Tutela del Territorio e del Mare, Istituto Superiore per la Protezione e la Ricerca Ambientale, Tipografia SCR–Roma.
- Svensson, L. 1992. Identification guide to European passerines. – British Trust for Ornithology.
- Swaddle, J. P. and Lockwood, R. 2003. Wingtip shape and flight performance in the European starling *Sturnus vulgaris*. – *Ibis* 145: 457–464.
- Swaddle, J. P. and Witter, M. S. 1997. The effects of molt on the flight performance, body mass and behavior of European starlings *Sturnus vulgaris*: an experimental approach. – *Can. J. Zool.* 75: 1135–1146.
- Szekely, T., Lislevand, T. and Figuerola, J. 2007. Sexual size dimorphism in birds. – In: Fairbairn, D. J., Blanckenhorn, W. U. and Székely, T. (eds), Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford Univ. Press, pp. 27–37.
- Thomson, R. L., Forsman, J. T., Sardà-Palomera, F. and Mönkkönen, M. 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. – *Ecography* 29: 507–514.
- Tyler, S. 2019. Water pipit *Anthus spinoletta*. – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. and de Juana, E. (eds), Handbook of the birds of the world alive. Lynx Edicions, accessed 30 January 2019.
- Vanhooydonck, B., Herrel, A., Gabela, A. N. A. and Podos, J. 2009. Wing shape variation in the medium ground finch *Geospiza fortis*: an ecomorphological approach. – *Biol. J. Linn. Soc.* 98: 129–138.
- Wilson, R. E., Valqui, T. H. and McCracken, K. G. 2010. Chapter 12: Ecogeographic variation in cinnamon teal *Anas cyanoptera* along elevational and latitudinal gradients. – *Ornithol. Monogr.* 67: 141–161.
- Zhu, H., Shi, J. P. and Zhao, C. J. 2005. Species composition, physiognomy and plant diversity of the tropical montane evergreen broad-leaved forest in southern Yunnan. – *Biodivers. Conserv.* 14: 2855–2870.
- Zuur, A. F., Ieno, E. N. and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. – *Methods Ecol. Evol.* 1: 3–14.