Differences in Wing morphology between juvenile and adult European Turtle Doves *Streptopelia turtur*: implications for migration and predator escape.

XABIER CABODEVILLA,^{1,2*} LARA MORENO-ZARATE² & BEATRIZ ARROYO²

¹*Department of Zoology and Animal Cell Biology, Faculty of Pharmacy, University of the Basque Country (UPV/EHU), Paseo de la Universidad 7, 01006 Vitoria-Gasteiz, Alava, Spain*

²*Instituto de Investigación en Recursos Cinegéticos (IREC) (CSIC-UCLM-JCCM). Ronda de Toledo 12, 13005 Ciudad Real, Spain*

*Corresponding author.
Email: xabier.cabodevilla@ehu.eus

Behaviour has direct links to wing morphology in bird species. Many studies have postulated migration to be one of the most important forces of selection acting on wing morphology, particularly in relation to wing pointedness. Studies in passerines have found that adults have longer and more pointed wings than juveniles, especially in migratory species. We analysed differences in wing morphology between age groups of the European Turtle Dove, a non-passerine migratory species that benefits from rounded wings during their daily activity, due to its ground-feeding behaviour and acrobatic flight style. Our results show that adults of this species have longer but more rounded wings than juveniles. This suggests that in this species wing morphology in juveniles is selected to facilitate the first migration, while other selection forces (e.g.,

flight manoeuvrability) are more important after the first moult. These data also explain why juveniles are not as adept at escaping from predators or hunters as adults.

Keywords: Age differences, predation risk, type of flight, wing pointedness, wing shape.

It is well known that wing morphology is associated with flight mode and is thus related to animal behaviour. Four main wing morphologies have been described in birds: (1) elliptical wings; (2) high aspect ratio wings; (3) dynamic-soaring wings; and (4) high-lift wings (Savile 1957, Hickman *et al.* 2008). The two more common wing morphologies, elliptical wings (no pointedness and convex) and high aspect ratio wings (pointed and concave), are commonly related to manoeuvrability and flight speed, respectively. Pointed wings are specialised for fast flight and long migrations. Studies comparing wing morphology between species, or between populations of the same species, exposed to different migration distances, have found a direct positive relationship between aspect ratio, wing pointedness and migration distance (Winkler & Leisler 1992, Senar *et al.* 1994, Norberg 1995, Lockwood *et al.* 1998, Pérez-Tris & Tellería 2001, Bowlin & Wikelski 2008, Milá *et al.* 2008, Vágási *et al.* 2016, Watanabe 2016). In contrast, convex wings are especially useful for closed turns, higher manoeuvrability and quick acceleration (Corvidae *et al.* 2006). These are typical in forest birds and predators that carry out certain types of foraging flights, and are very useful in helping to evade predators (Alatalo *et al.* 1984, Lockwood *et al.* 1998, Swaddle & Lockwood 1998). Convex wings enable faster take-off, at steeper angles, than pointed wings, which is important for species that feed on the ground (del Hoyo *et al.* 1997, Burns & Ydenberg 2002, Swaddle & Lockwood 2003).

Differences in wing morphology also occur among different age classes of birds. In general, juveniles of many species tend to have smaller wings than adults (Figuerola & Gutiérrez 2000, Nowakowski 2002, McKinnon *et al.* 2014, Furness & Furness 2016). Additionally, various studies have demonstrated that juveniles have more rounded wings than adults (Fernández & Lank 2007, Green *et al.* 2009, Milá *et al.* 2008, Arizaga & Barba 2011, de la Hera *et al.* 2014), as this age group requires greater stability and manoeuvrability to start flying (Alatalo *et al.* 1984). However, in relation to wing shape, results vary among species. For example, in the case of the Eurasian Reed Warbler *Acrocephalus scirpaceus*, Savi's Warbler *Locustella luscinioides* and Barn Swallow *Hirundo rustica*, adults have more rounded wings than juveniles (Nowakowski 2002, Peiró 2003, Huber *et al.* 2016). Reflective of neither of the above trends, for the Bearded Reedling *Panurus biarmicus* no significant differences in wing pointedness have been detected between juvenile and adult individuals (Peiró *et al.* 2006).

Most studies on morphological differences in wings between age groups have been carried out on passerines. However, ecological requirements of species are very diverse among bird groups; thus, it is possible that different selection forces affect wing morphology across different phylogenetic groups.

We investigated variation in wing morphology among juvenile and adult European Turtle Doves *Streptopelia turtur*. Pigeons and doves, one of the most diverse non-passerine orders, and are present all over the world with the exception of the Arctic and Antarctic (del Hoyo *et al.* 1997). Although this clade occupies several different habitats, its members have relatively conserved anatomy and morphology. In general, pigeons have larger flight muscles than other avian groups, reflecting their especially good flight abilities and flight speed of up to 60 km per hour (del Hoyo *et al.* 1997). They also have low aspect ratio wings, adapted for an explosive take-off, and relatively large and broad wings adapted for good manoeuvrability during flight, dodging to the left and right in close-order drill manoeuvres to evade predators (del Hoyo *et al.* 1997).

The European Turtle Dove is not an exception; like other pigeons, it is also very agile, with good manoeuvrability and acrobatic flights, and more or less rounded wings that allow for a strong and quick take-off (del Hoyo *et al.* 1997). Moreover, it is a trans-Saharan migrant (Eraud *et al.* 2013, Lormee *et al.* 2016) and is a reputed game species, hunted throughout its migration route (Marx *et al.* 2016).

We assess differences in wing morphology between juvenile and adult European Turtle Doves and discuss our results in the context of possible selection forces for migratory species that need a rounded wing for daily activity.

METHODS

Samples were collected during the European Turtle Dove (hereafter Turtle Dove) hunting season in Spain in 2016 (21 August to 21 September). During this time, we collected one wing from each of 746 hunted birds (438 juveniles and 308 adults) from 30 hunting areas distributed throughout south-central Spain (Fig. S1). The age of the sampled birds (juveniles, born the sampling year; and adults) was determined using moult criteria, following Demongin (2013).

Among all collected wings, we selected for measurement those that did not have more than two moulting primaries (i.e. wings with the most external eight primaries of the same generation present) and where the forearm and the external primaries were unbroken: 218 wings, from 19 hunting areas, fulfilled these criteria; 118 from juvenile and 100 from adult birds. We measured forearm (as an index of body size), wing length and the lengths of each of the eight most external primaries. The ninth primary (counting from the inside) was the longest in most (80%) individuals. Hereafter, for simplicity, when referring to 'the longest primary' we refer to P9.

We carried out a Size Constrained Components Analysis (SCCA), developed by Lockwood *et al.* (1998), using the length of each of the eight most external primaries for each individual. The SCCA is derived from a Principal Components Analysis (PCA), but

incorporates a rigorous geometric size model. In this analysis the first axis (C1) picks up the isometric size of the wing, and the rest of the components explain the differences in wing shape. The second axis (C2) can be interpreted as a measure of pointedness/roundness, and third (C3) as a measure of wing convexity (Table S1). This analysis was performed with the SAS 9.1 statistical package (SAS Institute 2002). All other analyses were carried out with R v3.4.0 (R Core Team 2017).

The origin of hunted birds can vary throughout the hunting period, as it is more likely that local birds are shot at the beginning of the hunting period, in August, than near the end in September, when many migrants from more northern populations may already be in Spain (Lormee *et al.* 2016, Marx *et al.* 2016). It is also possible that the origin of birds has an influence on wing morphology due to their different migration distances. We initially tested for whether there was a difference in wing length, forearm size or wing pointedness (C2) in relation to date of hunting. For this purpose, we used general linear models (GLM), fitting the dependent variables to a normal distribution, and including date (continuous variable) and age group (a two-level categorical variable) as explanatory variables.

Subsequently, with the aim of understanding possible differences in wing morphology between juveniles and adults, we carried out three sets of GLMs. 1) We tested whether wing length or the length of the longest primary varied among age groups, including forearm size as a covariate; i.e. we tested for age group differences taking into account body size. 2) We tested whether wing pointedness (C2) varied among age groups, using either wing length or forearm size as an additional covariate; i.e. we tested for age group differences taking into account body and wing size. 3) We tested whether the length of each individual primary varied among age groups, including either wing length or forearm size as an additional covariate; we calculated least square means for each age group (i.e. differences in primary length between juveniles and adults for the same wing length or same forearm size) using the library

lsmeans (Russell 2016) in R, and plotted these values for graphical representations of morphological differences for wings among age groups.

In all models the interaction between age and the continuous variable was initially included, but in all cases this interaction term was not significant ($P > 0.05$). We thus, excluded this variable and present only the results for direct effects.

RESULTS

We did not find significant changes in wing length, forearm or wing pointedness in relation to date ($F_{1,185} = 1.39$, $P = 0.24$; $F_{1,185} = 1.77$, $P = 0.19$; $F_{1,185} = 1.86$, $P = 0.17$ respectively). In contrast, age was a significantly explanatory factor for all three variables: adults had longer wings and forearms than juveniles ($F_{1,185} = 94.79$, $P < 0.001$; $F_{1,185} = 5.19$, $P < 0.05$, respectively) and more rounded wings ($F_{1,185} = 72.24$, $P < 0.001$) (Fig. S2).

When wing size comparisons between age groups were controlled for forearm size, the difference in wing length and the longest primary length between age groups remained significant ($F_{1,217} = 150.83$, $P < 0.001$; $F_{1,217} = 163.87$, $P < 0.001$, respectively; Fig. 1). The wings of adults were on average 6.06 mm longer than for juveniles, and the longest primary was on average 5.83 mm longer in adult versus juvenile Turtle Doves (Fig. 1).

In relation to wing morphology, longer wings were more pointed, but adults had more rounded wings than juveniles for a given wing length ($F_{1,217} = 88.53$, $P < 0.001$ for wing length; $F_{1,217} = 214.69$, $P < 0.001$ for age; Fig. 2). Similarly, for a given forearm length, we found the same differences in wing pointedness between ages, and wings with longer forearms were more pointed ($F_{1,217} = 105.82$, $P < 0.001$ for age; $F_{1,217} = 12.58$, $P < 0.001$ for forearm size; Fig. 2).

These differences in wing size and wing morphology are depicted in Fig. 3. There were significant differences between ages in the length of each primary when

controlling for forearm size (Table 1): all primaries were longer in adults than juveniles for a given body size (Fig. 3b). When controlling for wing length, differences in primary length between age groups varied in relation to primary order (Table 1). For a given wing length, length of the tenth primary was not significantly different among age groups, differences in P9 and P8 length were significant but small, whereas P7, P6 and P5 were clearly longer in adult than in juvenile Turtle Doves (Fig. 3a).

DISCUSSION

Our results show that, as in other species, the wings of adult Turtle Doves are longer than the wings of juveniles, but in contrast to other species, juvenile Turtle Doves have more pointed wings than adults. These results have direct implications for the flight of adults and juveniles and suggest that selection forces acting on the wing morphology of juvenile and adult Turtle Doves, or their relative importance between age groups, is different from that experienced in other species.

Adult Turtle Doves had longer wings than juvenile birds and surprisingly, significantly longer forearms. In altricial birds, the forearm, like other bones, has usually reached asymptotical size before fledging (Biljsma 1997, Brignon 1997). Differences in forearm size between ages can be found if sampled juveniles are primarily of different origins than sampled adults and if there are body size differences associated with the site of origin. However, given that no differences in size were found with date of hunting and the origin of the birds is not known, this hypothesis cannot be verified solely with the data from this study. Although we did not find a date effect on forearm length and wing shape, this does not mean that birds of different origins do not vary in size or morphology. There may not be a temporal segregation of migration from different populations. Future analyses of stable isotopes in feathers of sampled individuals may shed light on this topic. On the other hand, the forearm size differences among age groups found in this study might suggest a differential mortality in juvenile birds during

the first winter that favours larger individuals, but this should also be tested in future studies.

Our results indicate that the longer wings in adults in relation to juveniles are primarily a consequence of the increase in feather length after the first moult. However, not all primary feathers increase in the same proportion. The seventh, sixth and fifth primaries increase their length to a greater extent, whereas the tenth primary increases less than other feathers, resulting in a more rounded and convex morphology of the adult wing. Thus, in the case of the Turtle Doves and in contrast to other species, young birds have more pointed wings than adults.

In general, doves have rather rounded wings, which may be beneficial as this allows a strong take off and good manoeuvrability (del Hoyo *et al.* 1997). Because Turtle Dove feed on the ground, an acrobatic flight may be beneficial in evading predators. Their ground habits may exert an important selection force, favouring more rounded and convex wings. In contrast, it is possible that, for juvenile birds, surviving the first migration (which occurs shortly after fledging) is also a very strong selection force, favouring more pointed wings. All Turtle Doves finish their moult in the wintering areas (Demongin 2013). Juveniles, after finishing their first migration, moult wing feathers and acquire longer and more rounded wings. That the wings are rounder may not be beneficial in migration, but since they are also longer overall, the wing loading is lower and aspect ratio is higher, which makes them aerodynamically more efficient (Newton 2008) and hence, improves migration capacity. Therefore, our results suggest that the wings of juveniles are adapted for long-distance migration, but that predator avoidance becomes a more important selection force than migration for this species once the first migration has been achieved. This also indicates a possible explanation for the differences observed in forearm length between age groups: it is possible that smaller juveniles, with short and pointed wings, are not as effective at escaping predators, which would lead to higher mortality probabilities before the first winter.

In relation to the last point, these results also imply that juvenile birds are more prone to predation or hunting than adults (Swaddle & Lockwood 1998), as their wing morphology suggests slower take off and lower flight manoeuvrability. Indeed, it has been shown that a higher proportion of juveniles than adults are shot, which has been attributed to inexperience, less caution, and the slower escape response of juveniles (Rocha & Quillfeldt 2015). It would be important to determine whether different hunting modalities have differential impacts on population dynamics.

We would like to thank all hunters that collaborated with us, providing wings of hunted birds. Special thanks are due to Jose Francisco Lima, Maria Cruz Camacho, Yolanda Ramiro, Laia Casades and all workmates that helped to collect the samples in the field. Borja Milá and Rauri Bowie provided useful comments that improved the manuscript, and Sarah Young helped to revise the English.

REFERENCES

- Arizaga, J., & Barba, E.** 2011. Differential timing of passage of populations of migratory Blackcaps (*Sylvia atricapilla*) in Spain: evidence from flight-associated morphology and recoveries. *Ornis Fenn.* **88**: 104-109
- Alatalo, R. V., Gustafsson, L., & Lundbäck, A.** 1984. Why do young passerine birds have shorter wings than older birds?. *Ibis* **126**: 410-415.
- Biljsma, R. G.** 1997. *Handleiding veldonderzoek Roofvogels*. Utrecht: KNNV Uitgeverij.
- Brignon, A-L.** 1997. *Croissance et métabolisme chez des poussins de busard cendré (*Circus pygargus*) élevés en captivité*. PhD, Ecole National Veterinaire de Nantes, Université de Nantes.
- Bowlin, M. S., & Wikelski, M.** 2008. Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. *PLoS ONE* **3**: e2154.

- Burns, J. G., & 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.
- Corvidae, E. L., Bierregaard, R. O., & Peters, S. E.** 2006. Comparison of wing morphology in three birds of prey: correlations with differences in flight behavior. *J. Morphol.* **267**: 612-622.
- del Hoyo, J., Elliot, A., & Sargatal, J.** 1997. *Handbook of the Birds of the World*, Vol. 4. Barcelona: Lynx Ediciones.
- de la Hera, I., Pulido, F., & Visser, M. E.** 2014. Longitudinal data reveal ontogenetic changes in the wing morphology of a long-distance migratory bird. *Ibis* **156**: 209-214.
- Demongin, L.** 2013. *Guide d'identification des oiseaux en main. Les 250 espèces les plus baguées en France.* Beauregard-Vendon.
- Eraud, C., Rivière, M., Lormée, H., Fox, J. W., Ducamp, J. J., & Boutin, J. M.** 2013. Migration routes and staging areas of trans-Saharan Turtle Doves appraised from light-level geolocators. *PLoS ONE* **8**: e59396.
- Fernández, G., & Lank, D. B.** 2007. Variation in the wing morphology of Western Sandpipers (*Calidris mauri*) in relation to sex, age class, and annual cycle. *Auk* **124**: 1037-1046.
- Figuerola, J. & Gutiérrez, R.** 2000. Why do juvenile Moustached Warblers have shorter wings?. *Ornis Fenn.* **77**: 183-187.
- Furness, E. N., & Furness, R. W.** 2016. Influences of feather wear and age on wing lengths of Blue Tits *Cyanistes caeruleus*. *Ring. Migr.* **31**: 1-5.
- Green, D. J., Whitehorne, I. B., Taylor, A. L., & Drake, E. L.** 2009. Wing morphology varies with age but not migratory habit in American Dippers. *Wilson J. Ornithol.* **121**: 141-147.
- Hickman, C. P., Roberts, L. S., Keen, S. L., Larson, A., l'Anson, H., & Eisenhour, D. J., Ober, W. C., Garrison, C. W.** 2008. *Integrated principles of zoology* (14thed). New York: McGraw-Hill.

- Huber, G. H., Turbek, S. P., Bostwick, K. S., & Safran, R. J.** 2016. Comparative analysis reveals migratory swallows (Hirundinidae) have less pointed wings than residents. *Biol. J. Linn. Soc.* **120**: 228-235
- Lockwood, R., Swaddle, J. P., & Rayner, J. M.** 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *J. Avian Biol.* **29**: 273-292.
- Lormee, H., Boutin, J. M., Pinaud, D., Bidault, H., & Eraud, C.** 2016. Turtle Dove *Streptopelia turtur* migration routes and wintering areas revealed using satellite telemetry. *Bird Stud.* **63**: 1-5.
- Marx, M., Korner-Nievergelt, F., & Quillfeldt, P.** 2016. Analysis of Ring Recoveries of European Turtle Doves *Streptopelia turtur*-Flyways, Migration Timing and Origin Areas of Hunted Birds. *Acta Ornithol.* **51**: 55-70.
- McKinnon, E. A., Fraser, K. C., Stanley, C. Q., & Stutchbury, B. J.** 2014. Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. *PLoS ONE* **9**: e105605.
- Milá, B., Wayne, R. K., & Smith, T. B.** 2008. Ecomorphology of migratory and sedentary populations of the yellow-rumped warbler (*Dendroica coronata*). *Condor* **110**: 335-344
- Newton, I.** 2008. *The migration ecology of birds*. Elsevier: Amsterdam.
- Norberg, U. M.** 1995. Wing design and migratory flight. *Isr. J. Zool.* **41**: 297-305.
- Nowakowski, J.** 2002. Variation of morphometric parameters within the Savi's Warbler (*Locustella luscinioides*) population in eastern Poland. *Ring* **24**: 49-67.
- Peiró, I. G.** 2003. Intraspecific variation in the wing shape of the long-distance migrant Reed Warbler *Acrocephalus scirpaceus*: effects of age and distance of migration. *Ardeola* **50**: 31-37.
- Peiró, I. G., Robledano, F., & Esteve, M. A.** 2006. The effect of age and sex on wing morphology and body size of the Bearded Tit *Panurus biarmicus* in relation to complete moult. *Ring & Migr.* **23**: 101-106.

- Pérez-Tris, J., & Tellería, J. L.** 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *J. Avian Biol.* **32**: 207-213.
- R Core Team** 2017. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. URL <https://www.Rproject.org/>.
- Rocha, G., & Quillfeldt, P.** 2015. Effect of supplementary food on age ratios of European turtle doves (*Streptopelia turtur* L.). *Anim. Biodiv. Conserv.* **38**: 11-21.
- Russell, V. L.** 2016. Least-Squares Means: The R Package lsmeans. *J. Stat. Softw.* **69**: 1-33.
- SAS Institute, Inc.** 2002. SAS Online Doc: Version 9.1. Cary, NC, USA.
- Savile, D. B. O.** 1957. Adaptive evolution in the avian wing. *Evolution* **11**: 212-224.
- Senar, J. C., Lleonart, J., & Metcalfe, N. B.** 1994. Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. *J. Avian Biol.* **25**: 50-54.
- Swaddle, J. P., & Lockwood, R.** 1998. Morphological adaptations to predation risk in passerines. *J. Avian Biol.* **29**: 172-176.
- Swaddle, J. P., & Lockwood, R.** 2003. Wingtip shape and flight performance in the European Starling *Sturnus vulgaris*. *Ibis* **145**: 457-464.
- Vágási, C. I., Pap, P. L., Vincze, O., Osváth, G., Erritzøe, J., & Møller, A. P.** 2016. Morphological Adaptations to Migration in Birds. *Evol. Biol.* **43**: 48-59.
- Watanabe, Y. Y.** 2016. Flight mode affects allometry of migration range in birds. *Ecol. Lett.* **19**: 907-914.
- Winkler, H., & Leisler, B.** 1992. On the ecomorphology of migrants. *Ibis* **134**: 21-28.

Supporting Online Material (SOM)

Table S1. Results of SCCA analysis of the primary feathers.

	C1	C2	C3
P10	0.396	-0.633	-0.244
P9	0.392	-0.407	0.073
P8	0.372	-0.158	0.311
P7	0.332	0.221	0.500
P6	0.332	0.293	0.321
P5	0.327	0.327	0.006
P4	0.330	0.311	-0.581
P3	0.338	0.265	-0.384
% total variance explained	92.67	4.66	1.06
% shape variance explained		63.67	14.44

Figure S1. Number of samples used in the study in relation to the province of collection. The number of adults (A) and juveniles (J) samples each province are also specified.

Figure S2. The relationship between wing length, forearm size and wing roundedness, and date of collection (Date: 0 = 21 of August; 32 = 21 of September). Adults are represented by black dots (continuous line) and juveniles by white dots (discontinuous line).

Tables

Table 1. Statistical results of the comparisons between ages for each primary feather and corrected for wing length and forearm size. Degrees of freedom are 1, 217 in all cases.

	Corrected for wing length		Corrected for forearm	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
P10	0.17	0.68	112.44	<0.001
P9	18.16	<0.001	163.87	<0.001
P8	87.45	<0.001	258.79	<0.001
P7	335.92	<0.001	553.38	<0.001
P6	280.26	<0.001	528.34	<0.001
P5	261.68	<0.001	520.49	<0.001
P4	155.97	<0.001	390.24	<0.001
P3	129.07	<0.001	345.94	<0.001

Figure Legends

Figure 1. Relationship between forearm size and wing length (a) and length of the longest primary (b).

Adults are represented by black dots (continuous line) and juveniles by white dots (discontinuous line).

Figure 2. Relationship between wing roundedness and wing length (a) and forearm size (b). Adults are represented by black dots (continuous line) and juveniles by white dots (discontinuous line).

Figure 3. Graphic representation of the differences in wing shape between juvenile and adult European Turtle Doves: least square means of the length of primary feathers for adults (black dots) and juveniles (white dots), controlling for wing length (left) or forearm size (right). The numbers next to the black dots indicate the difference (mm) between adult and juvenile feather length.

Figures