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Feathers for escape: the transition from juvenile to adult in red-legged partridges (*Alectoris rufa*)

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Almost all birds use their fight feathers as a means of escaping predators, and their specific design is adapted to their individual circumstances. For example, Galliform birds use a fast, explosive, noisy take-off to startle a predator. Their legs, wings and feathers must work together to create a strong propulsive force and loud, rhythmic sound. Partridges in a group initiate escape simultaneously, even though individuals in the flock differ in size and experience, as well as in age and sex resulting in feathers that differ in length and shape. In a long-term study, we measured 13 814 wild red-legged partridges (*Alectoris rufa*) to understand how variation in feather proportions and morphometrics between the age–sex classes relate to their escape abilities. We devised two new indexes to quantify the aerodynamic differences between age–sex classes. Our approach synthesizes the understanding of bird take-flight mechanics, feather proportions and the aerodynamic properties of wing tips to show how differences in feather length and tip shape characterize age–sex classes. Our findings suggest that the density, stiffness, permeability, size and shape of the distal primary feathers and wing tips can explain aerodynamic differences between individuals and the efficiency of groups in escape situations.

ADDITIONAL KEYWORDS: distal primary feathers – feather tip – flock coordination – predator escape – take-off – wing tip.

INTRODUCTION

Group living is a common strategy for surviving to the attacks by predators (Møller *et al.*, 2016), and groups of prey species typically include individuals of different ages and sexes (Aplin *et al.*, 2013). Individuals in a group learn to improve their escape abilities throughout their lives, and their growing experience increases the ability of their group to avoid and survive predator attacks (Santos *et al.*, 2015; Noguera, Kim & Velando, 2017). Prey animals must generally forage while simultaneously watching out for, and avoiding, predator attacks (Hudin *et al.*, 2016). As a first strategy, birds maintain a secure distance from predators, but when predators approach, they take flight and search for cover (Møller, Vágási & Pap, 2013).

During high-risk situations, such as a predator attack, partridges exhibit a powerful jump using their legs and then flap their wings to take flight (Tobalske & Dial, 2000). This ability to initiate a quick escape allows partridges to successfully foil predator attacks, the explosive take-off providing sufficient inertia to become airborne as well as generating a burst of noise that startles predators (Niese & Tobalske, 2016; Tobalske, Jackson & Dial, 2017). To take flight, a partridge must generate enough lift and thrust to lift their weight and then thrust them forwards. This explosive type of take-flight is known as 'burst flight' (Askew & Marsh, 2002). During take-off, the stroke amplitude of the wings is at a maximum, while in sustained and descending flight, the stroke amplitude decreases (Hedenström, 2002), the power requirements being less for steady flight than for take-off (Earls, 2000).

This specialized form of take flight is facilitated by the shape of the wing tip, specifically the shape and

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properties of the distal primary feathers (Nudds, Kaiser & Dyke, 2011). The wing surface, shape and a bird's weight set the basic aerodynamic constraints for flight (Henningsson, Hedenström & Bomphrey, 2014), so that the relationships between total wing length, primary feather length and weight define various aspects of flight performance (Muijres *et al.*, 2012; Klaassen van Oorschot, Tang & Tobalske, 2017). Feather structure is also influenced by the flight habit of a species. Birds with a strong flapping flight have more robustly constructed primary feathers, with a relatively greater rachis width and barb density (Pap *et al.*, 2015). The distal primaries are more heavily loaded than the innermost ones and have a more prominent tip because thrust is largely generated by the distal parts of the wings (Butler, 2015). In addition, the three distal primaries are able to flex independently and so achieve greater velocity (Wang *et al.*, 2012), and their tips differ in their air permeability and aerodynamic properties (Muller & Patone, 1998). Air passes more easily through the vanes of more permeable feathers due to their less barb and barbule density, and the less adhesive properties of the hamuli (hooks), while feather stiffness is related to more dense vanes the width and wall thickness of the rachis (Feo *et al.*, 2015).

The red-legged partridge (*Alectoris rufa*) (hereafter, partridge) is a key prey species in Mediterranean ecosystems (Potts, 2012). Males and females differ in body size and form, and individual size is also related to age and hierarchical rank. Thus, age–sex class, body condition and rank are interrelated and define an individual's role within and between social groups (Alkon, 2015). As birds age, their locomotor capacity and aerodynamic performance increase. Flight feather morphology also changes in the ontogenic transition from young to fully mature individuals (Heers, Tobalske & Dial, 2011). We can expect scaled body parameters and balanced aerodynamic performance among age–sex classes because successful escape from predators requires equivalent flight capacity in both juveniles and adults of both sexes. Juveniles and females have less mass, while adults and males are larger, requiring the need to compensate for increased weight with greater muscular power and larger wing surfaces to achieve a similar flight speed (Tobalske *et al.*, 2017). We can expect that juveniles and females, being smaller, may be better fliers. However, there is practically no data on how the sizes of the various wing parameters change with age–sex class in partridges.

The tip form, slot shape and dihedral angle of the distal primaries have aerodynamic consequences and exert a remarkable influence on flight performance (KleinHeerenbrink, Johansson & Hedenström, 2017) Birds with pointed wing shapes fly more rapidly, and those with blunt wing shapes show greater manoeuvrability (Norberg, 1979; Saino *et al.*, 2017). Flight velocity and manoeuvrability also depend on the power of flapping and the aerodynamic characteristics of the body. We can, therefore, expect relatively pointed wing tips in young partridges and relatively rounded wing tips in older partridges, larger primary feathers in males than in females, since velocity and manoeuvrability of an individual are influenced by its age- and sex-related size and weight (Fernández *et al.*, 2007; De la Hera, Pulido & Visser, 2014).

In this study, we examined how the proportion and morphometric variation between partridge age–sex classes can influence their escape abilities. We used biometric data obtained during a long-term study of a wild partridge population in southern Spain. Our objectives were to (1) examine whether different partridge classes have distinct feather length and tip shape and (2) evaluate wing-tip shape and surface–weight ratio (two indices indicating the aerodynamic capacities of different age–sex classes).

MATERIAL AND METHODS

Study area and data collection

We examined hunted wild partridges from 'Las Ensanchas', a hunting estate in the Jabalón River basin in Ciudad Real, Spain (38°39′N, 3°13′W, 790–840 m a.s.l.). The habitat type is Mediterranean *dehesa*, composed of open woodland (*Quercus ilex*) with an understory of shrubland (25%) interspersed with pastures and cultivated land (75%). We studied recently shot birds between 1998 and 2011 as a representative sample of the whole population. Age was determined by examining the primary feathers (colour and wear) and sex by spur characteristics (Nadal, Ponz & Margalida, 2016). We measured weight in the field using a digital weight scale with a 1-g precision and body length from beak tip to tail with the body flattened to a ruler. One wing was taken from each bird (cut through the ulna-radius) and prepared for laboratory measurements. The wings were combed and washed if necessary and then dried for 15 days in an oven at 40 °C.

We recorded wing length (from wrist to wing tip with the wing folded, and placed flat on a ruler), eighth, ninth and tenth primary feather lengths (from tip to integument insertion, with feather flattened on a ruler), all to the nearest 0.5 mm. The measurements were repeated to confirm the value obtained. One of us (J.N.) performed all of the field measurements and the other researcher (C.P.) performed all of the laboratory measurements. Across 14 years, we examined 13 814 wild partridges, 77% collected in October, 20% in November and 3% in December. Not all of the

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partridges examined were useful for all parameters (i.e. some birds were mutilated, lacked certain body parts or had broken or moulting feathers). These individuals were eliminated from the analysis of the variable affected.

Wing-tip shape and surface–weight indexes

The wing-tip shape was analysed using feather parameters *A* and *B*: *A* = the ninth primary length minus tenth primary length and *B* = the eighth primary length minus the ninth primary length. Wing-tip shape was quantified using the sizes of the two parameters *A* and *B*. When the parameters *A* and *B* are similar, the wing tip is pointed; when *B* is less than *A*, the wing tip is blunt (Fig. 1). We performed a regression between *A* and *B* for each age–sex class and used the *A*/*B* ratio as an index of wing-tip shape (Lees, Dimitriadis & Nudds, 2016). We used an index of mass relative to size of juvenile females; the average mass of each class divided by the average of juvenile female mass. We used an index of experience relative to juvenile females; the age in months of each class divided by the age in months of the juvenile female, because life expectancy is lower in this age–sex class. Accordingly, this index could be considered as a surrogate of the accumulated experience.

To assess the flight characteristics of each partridge age–sex class, we performed a regression analysis between weight (as an index of load) and total length by wing length (as a surface index that is proportional to half of the bird surface). Hence, the ratio of total length by wing length to weight provides an index of aerodynamic value and indicates the flight properties of each age–sex class (Hedenström, 2002).

Statistical analyses

One-way analysis of variance was used to test primary feather length differences between all age–sex classes. We performed isometric functions with simple regression models to explain the weight or wing length with respect to eighth, ninth and tenth primary lengths and with respect to surface index (total length by wing length). We performed allometric functions with logarithmic transformation of data (Supporting Information, Tables S1–S3). We used corrected Akaike information criterion (AICc) to select between isometric (maintains the proportion) or allometric (changes the proportion) functions (Burnham & Anderson, 2002), and we used power equations to disclose allometric relationships between weight and primary length and between wing and primary length. In the dataset, we performed simple and multiple regression models including age–sex class as factor. We performed analysis of covariance to assess differences between age–sex classes (SAS, 2015).

RESULTS

A total of 9938 partridges (72% of those collected) were used for weight measurements: 7529 (54%) for total length, 11 539 (83.5%) for wing length and 11 844

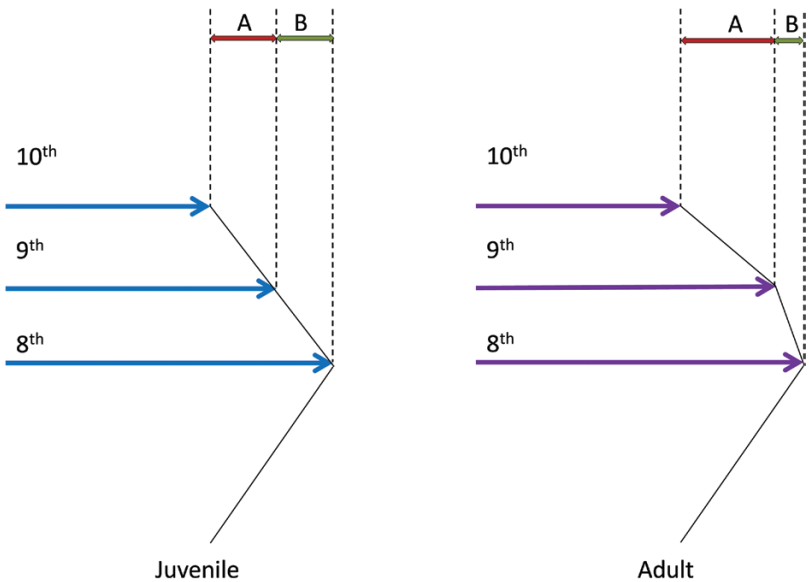

Figure 1. Wing tip, formed by the apices of the eighth, ninth and tenth primaries. *A* = ninth minus tenth primary length; *B* = eighth minus ninth primary length. In young partridges, a pointed wing shape is indicated, and in old partridges, a blunt wing shape is indicated.

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(85.7%) for tenth primary length, 13 011 (94.2%) for ninth primary length and 10 696 (61.4%) for eighth primary length. All variables showed significant differences between age–sex classes (Fig. 2 and Table 1). All of the feather lengths were scaled between age–sex classes in the following order: juvenile female < adult female < juvenile male < adult male. Between pairs of variables, the allometric functions had lower AICc than isometric functions. We found power equations between weight and the tenth primary length $y = 0.04X^{2.01}$, and the ninth primary length $y = 0.08X^{1.85}$, and the eighth primary length $y = 0.02X^{2.09}$, and between wing length and the tenth primary length $y = 6.4X^{0.7}$, and the ninth primary length $y = 7.7X^{0.65}$, and the eighth primary length $y = 4.2X^{0.77}$ (Supporting Information, Tables S1–S3).

Considering all individuals, A and B were negatively correlated ($R^2 = 0.25$, $P < 0.001$, $N = 8204$). The regression of A explained by B of adult males had a

Table 1. Differences in primary length between age–sex classes (juvenile female, adult female, juvenile male and adult male) of the red-legged partridge by analysis of variance

	N	F	P
Tenth primary length	11 844	7725.5	< 0.0001
Ninth primary length	13 011	11 651.8	< 0.0001
Eighth primary length	10 696	7668.6	< 0.0001

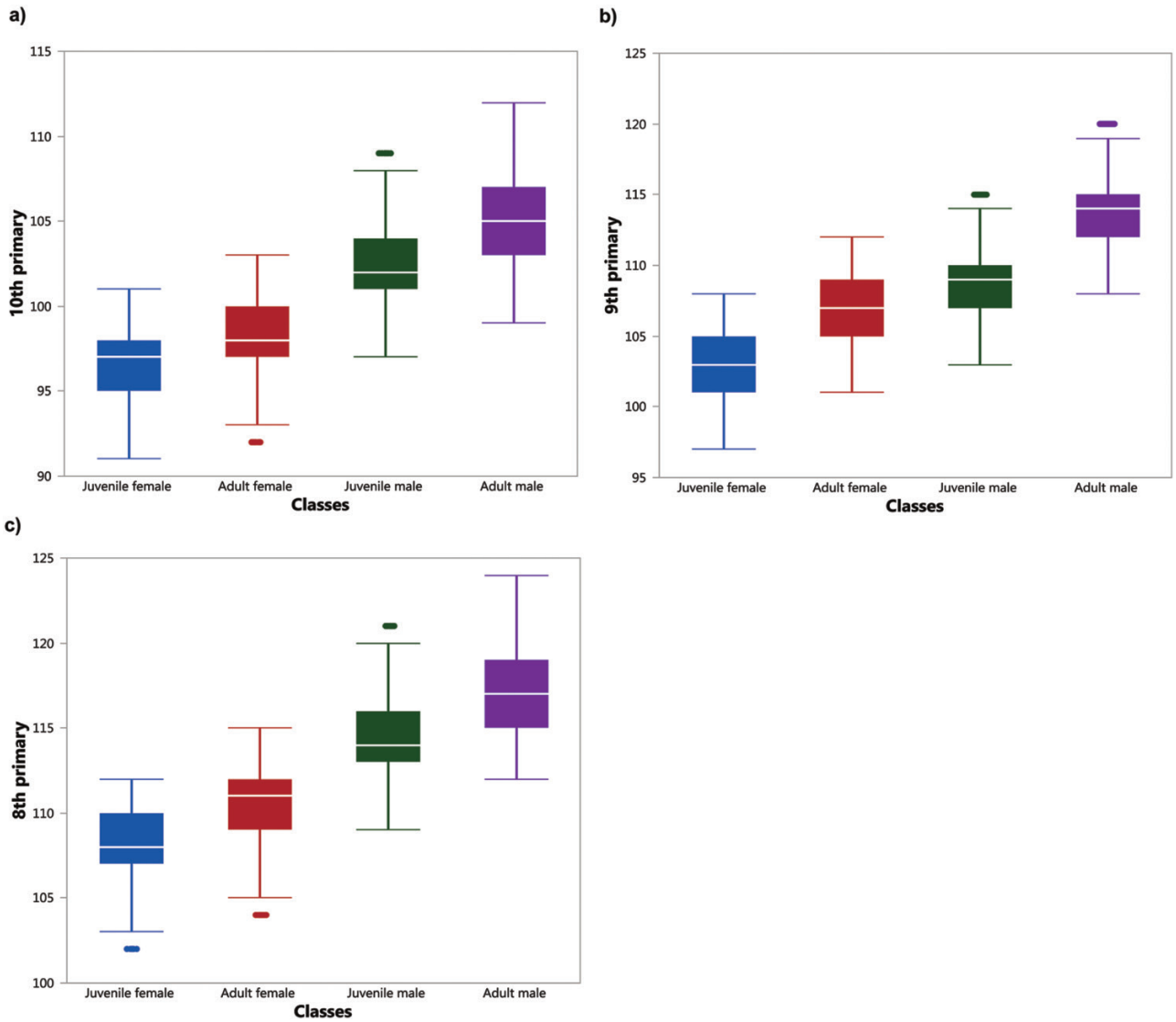

Figure 2. Scaled body differences among feathers (a = tenth primary, b = ninth primary, c = eighth primary) measured in millimetres between age–sex classes (juvenile female, adult female, juvenile male and adult male) in the red-legged partridge.

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similar slope (b = −0.30 ± 0.02) compared with adult females (b = −0.32 ± 0.04), as did juvenile males (b = −0.17 ± 0.02) compared with juvenile females (b = −0.22 ± 0.02). This indicates that the wing tip is rounded in old birds and pointed in young birds (Figs 1, 3 and Table 2) and that the A/B ratio separates younger birds from older birds (Table 3).

Overall, considering age–sex class as factor, weight was positively related to total length × wing length, followed a linear model (R^2 = 0.77, P < 0.001, N = 6337). The regressions for the age–sex classes were as follows: juvenile females (R^2 = 0.19, P < 0.001, N = 1547), juvenile males (R^2 = 0.26, P < 0.001, N = 1318), adult females (R^2 = 0.16, P < 0.001, N = 1594) and adult males (R^2 = 0.19, P < 0.001, N = 1878). The global model showed significant interactions (slopes differences) among the age–sex classes. Regressions of adult males had a similar slope (b = 0.0060 ± 0.0003) to juvenile males (b = 0.0068 ± 0.0003), adult females (b = 0.0052 ± 0.0003), to juvenile females (b = 0.0056 ± 0.0003). Females had a greater (total length × wing length)/weight ratio than males (Fig. 4 and Table 3).

DISCUSSION

Our results show that the size of the outermost primaries is scaled among partridge age–sex classes (Martin, 2015). The various age–sex classes show scaled proportions in accordance with their differing flight abilities, social roles and positions in the social hierarchy (Jackson, Segre & Dial, 2009; Crates *et al.*, 2016). Scaled primary proportions between age–sex classes is, therefore, a consequence of maturation and sexual size dimorphism (Heers *et al.*, 2016). Maturation in partridges involves fattening, an increase in the thickness of the integument, increasing ossification and stronger feathers (Homberger & de Silva, 2003; Piersma & Drent, 2003). Our findings suggest that interpretations of size, form and functional attributes must take scaling effects among age–sex classes into account (McFarlane, Altringham & Askew, 2016).

Use of the legs and wings enables birds to take flight to avoid predators (Tobalske & Dial, 2007). Because juvenile females have lighter pectoral muscles for flapping, they depend more on their surface–weight proportions and wing-tip shape to achieve a similar flight speed to adult males (Jackson, Tobalske & Dial, 2011). Hens and juvenile birds weigh less and therefore do not need the same pectoral power as adult males to achieve a similar speed flight (Tobalske, Hedrick & Biewener, 2003). A higher mortality rate would be expected for a certain age–sex class, compared to others, if it could not fly as efficiently. By living in groups, partridges take advantage of flock experience and ability to escape from predators. Thus, the anti-predator behaviour of flock must compensate for some of these individual differences in flight capacity (Macleod *et al.*, 2005; Rogers, 2015).

All age–sex classes showed a negative regression between A and B parameters probably because these two indexes are complementary. The regression lines for A–B in adults showed a more pronounced slope than in juveniles (Fig. 3), implying a more rounded wing tip (Wang & Clarke, 2015). With maturation, wing-tip shape changes from a more pointed form

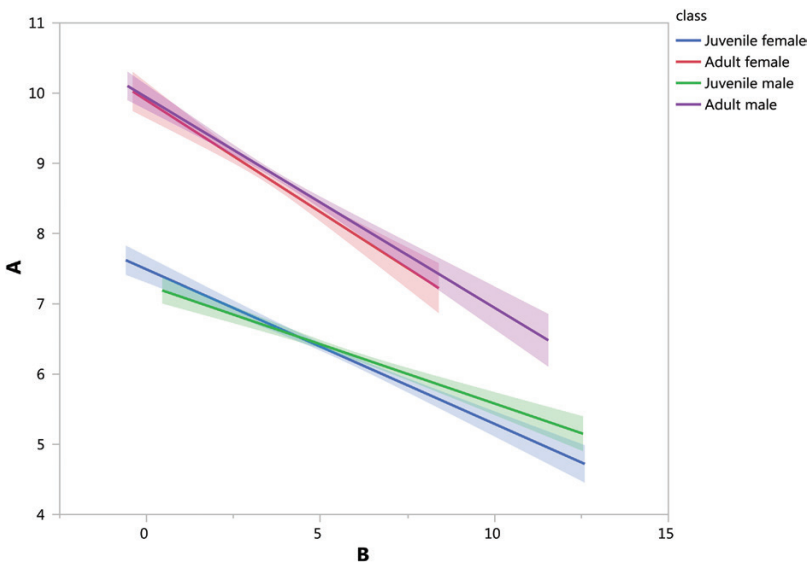

Figure 3. Wing-tip shape index and the regression between A and B segments in each age–sex class.

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Table 2. Shape and properties of the eighth, ninth and tenth primary feather apices in partridge age–sex classes

	Apex consistency	Apex shape	Raquis stiffness	Shape of wing tip
Juvenile female	Permeable	Pointed	Flexible	Pointed
Juvenile male	Permeable	Pointed	Flexible	Pointed
Adult female	Impermeable	Rounded	Stiff	Rounded
Adult male	Impermeable	Rounded	Stiff	Rounded

Table 3. Indexes of wing, surface–weight, muscle development and experience in partridge age–sex classes

	Wing-tip shape index	Surface–weight index	Index of mass with regard to the juvenile female	Index of experience with regard to the juvenile female
	A/*B*	(total length × wing length)/weight		
Juvenile female	1.43	130.8	1	1
Juvenile male	1.29	122.9	1.19	1
Adult female	2.87	130.5	1.04	> 4
Adult male	2.74	121.2	1.25	> 4

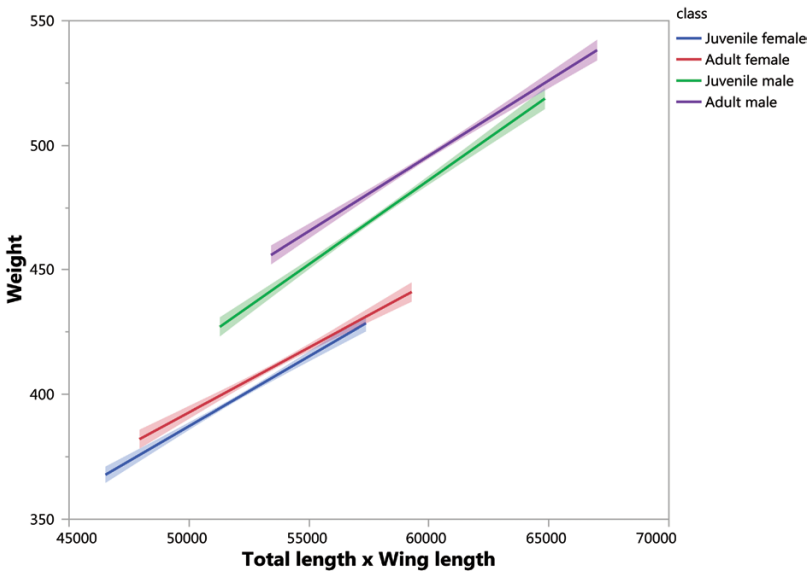

Figure 4. Aerodynamic index and the regression between weight and total length × wing length in each age–sex class.

in juveniles (for increased flight velocity) to a more blunt form in adults (for better flight manoeuvrability) (Heers & Dial, 2015). There is a clear relationship between feather morphology and aerodynamic performance, with older birds having stiffer distal primaries, a higher number of barbicels and a higher degree of overlap between barbules (Heers, 2016). These characteristics generate greater lift/drag ratios than in juvenile wings, which have flexible rachis and less cohesive barbules (Schmitz *et al.*, 2015). Wing tips show different slot patterns and feather apical form in the different age classes, causing changes in drag, lift, stiffness, flapping power and flight capacity (Hahn *et al.*, 2016). Aerodynamic forces put more pressure on the distal feathers in flapping flyers, and selection pressures drive flight feather form towards the most functional morphology. In young birds, the ninth and tenth distal primary feathers are light, flexible and pointed, while in adults, they are rounder, stiffer and have denser vanes (Dawson, 2005).

Efficacy (i.e. successful escapes) is more important than efficiency (i.e. aerodynamic performance) in escaping predators. Therefore, various mechanical, physiological and behavioural mechanisms combine

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to equalize the different age–sex classes in terms of escape efficacy (Moore & Biewener, 2015). The surface–weight index might be useful in understanding the flight capacity differences among bird classes. For example, males are heavier and have worst aerodynamic indexes and can compensate for this with larger pectoral muscles, longer wings and stiffer distal feathers (Usherwood, 2016).

In this study, we highlight the attributes of feathers, which improve predator escape efficiency in partridges. Flock success also depends on a coordinated response; simultaneous take-off, flight and landing combine to give significant advantages against predator attacks. Social status, individual maturity and sex influence the cohesive activities of a group of partridges, and thus their survival prospects.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Results of covariance and regression analysis.
Table S2. Results of covariance and regression analysis (logarithmic transformation of data).
Table S3. Results of isometric and allometric (logarithmic transformation) regression models for weight and surface index.

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