A potential trade-off between wing morphology and colouration for improved flight efficiency in the Larinae

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Article

Keywords:

Posted Date: May 17th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1638619/v1

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Version of Record: A version of this preprint was published at Communications Biology on November 22nd, 2022. See the published version at https://doi.org/10.1038/s42003-022-04144-8.
Abstract

There are many hypotheses explaining the diversity of colours and patterns found in nature, but they are often difficult to examine empirically. Recent studies show the dark upperside of the wings of gliding birds could reduce drag by decreasing the density of surrounding air. It may therefore be expected that species with darker wings have less efficient wing morphology than their paler counterparts. I conducted a phylogenetic comparative analysis of the Larinae (gulls) to test whether wing loading is a predictor of wing darkness. I found that, for each standard deviation increase in wing loading, wing darkness is predicted to increase by 1.2 shades on the Kodak grey scale. Wing darkness is also negatively correlated with the distance from the equator of species’ breeding and resident ranges. Furthermore, heavier species have lower aspect ratio wings, suggesting that dark wings have evolved to improve the trade-off between maneuverability and long distance flight.

Introduction

A great number of hypotheses have been proposed to explain the diversity in patterns and colours in the animal kingdom, and biologists continue to debate the adaptive significance of pigmentation and markings. For example, the function of the black and white stripes of zebra has long been debated, with many popular hypotheses not withstanding analysis\(^1\). Some phenomena have received a lot of attention: it is well-established that camouflage plays an important role in disguising animals both from predator and prey\(^2\). Countershading, whereby the upperside of an organism is dark while the underside is pale, appears to allow animals to be concealed from both dorsal and ventral viewpoints: a pale underside blends in against a bright sky, while a dark upperside is less conspicuous against a backdrop of land or sea\(^3\). This colouration has evolved independently several times in various seabirds, suggesting an adaptive role\(^4\).

While it is easy to understand the benefits of countershading, the function of other, similar, colour patterns are less clear. For instance, most species of the Larinae (gulls) are white, and the majority have a grey upper wing and back, which is often referred to as the mantle\(^5\). However, the nape, rump and tail are usually also white, making countershading an unsatisfactory explanation. Melanin, the pigment that produces the grey colour, is thought to be energetically costly to produce\(^6,7\), so it is likely that this pattern has arisen and been maintained through selection. Melanin has many functions, including protection of feathers against damaging ultraviolet radiation\(^8\). Indeed, Dufour et al.\(^9\) recently found a positive effect of insolation (incident solar radiation) on Larinae mantle darkness.

Wing colouration may, however, be explained by additional factors. Hassanalian et al.\(^10,11\) showed that, because dark surfaces absorb heat, thus decreasing the density and increasing the viscosity of air flowing over them, the dark wing colour of many gliding birds may function to reduce drag by decreasing the amount of friction generated during flight. A recent analysis of seabirds\(^4\) found that wing darkness is associated with morphology optimized for flight efficiency. However, this analysis was conducted at a
broad scale, and morphology differs within and among taxonomic groups. Furthermore, for most seabird groups, wing loading and aspect ratio appear to be positively correlated, whereas previous estimates indicate that it is negatively correlated for Larids such as gulls\textsuperscript{12}. This may be because of differences in foraging behaviour, with gulls generally taking shorter foraging trips than other seabirds\textsuperscript{12}. High aspect ratio wings, possessed by birds that have a long wingspan compared to wing breadth, are associated with flight efficiency because they create less induced drag, whereas low aspect ratio wings permit better maneuverability\textsuperscript{13}. Additionally, high wing loading, a bird's body mass per unit of wing area, results in a lower production of lift\textsuperscript{13}. Birds must produce more lift than drag to remain in flight\textsuperscript{14}, and there is likely to be a trade-off between adaptation for maneuverability and for long distance gliding.

Gulls are an excellent system with which to test the hypothesis that wing darkness is related to flight efficiency. They share relatively similar morphology and ecology, but show striking variation in mantle darkness and body size. For instance, one species, the Ivory Gull (\textit{Pagophila eburnea}), is completely white, while others, notably large species such as the Great Black-backed Gull (\textit{Larus marinus}) and Pacific Gull (\textit{L. pacificus}), have almost black mantles. I hypothesized that the dark mantle colouration of gulls functions to reduce drag, and that species with darker mantles have evolved this pattern as a means of compensating for reduced flight efficiency derived from constraints on wing morphology. Therefore, I predicted that the variation in mantle darkness could be explained, at least in part, by species’ wing loading, with relatively heavier species possessing darker mantles.

I calculated the wing loading and aspect ratio of almost all recognized species of gull (N = 50; see Methods) and considered (a) the effect of wing loading on mantle darkness, and (b) whether species with high wing loading have lower aspect ratio wings. To ensure that any relationship between wing loading and mantle darkness was not simply a consequence of shared ancestry, I ran four different models, each assuming a different model of evolution, for comparison: a non-phylogenetic (NP) model (an ordinary least squares regression), a Brownian motion (BM) model (which assumes traits evolve via a random walk), an Ornstein-Uhlenbeck (OU) model (which constrains the evolution of traits towards an optimum) and Pagel's lambda model (which transforms the tree branches according to estimated phylogenetic signal in trait covariance). As the selection pressure generated by insolation\textsuperscript{9} may obscure or confound an effect of wing loading, I incorporated this as a variable in the model. Insolation is directly related to the distance from the equator\textsuperscript{15}, thus I converted the centroid latitudes of each species’ breeding and resident range to absolute values.

Results

1. Wing loading predicts an increase in mantle darkness

Wing loading ranged from 0.002 to 0.007 g mm\textsuperscript{-1} and was associated with an increase in mantle darkness across the four tested models. The OU model provided a significantly better fit of the data than either the NP or the BM model (Table 1). The lambda model did not fit the data significantly better than
the NP model (Table 1). The phylogenetic half-life estimated by the OU model was 0.026, which suggests a small but non-trivial influence of phylogeny on the measured traits, and selection towards an optimal value of mantle darkness over evolutionary history (Fig. 1).

Both wing loading and absolute latitude had statistically significant effects on mantle darkness. The OU model estimated a positive increase on the Kodak Grey Scale (KGS) of $1.22 \pm 0.51$ SE for each standard deviation increase in wing loading (Table 1, Fig. 2a). Conversely, for each degree increase in distance from the equator, a reduction in mantle darkness equivalent to $-0.07 \pm 0.03$ SE on the KGS was estimated (Table 1, Fig. 2b).

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimate ± SE (P-value)</th>
<th>Log Likelihood</th>
<th>LRT P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ornstein-Uhlenbeck (OU)</td>
<td>$\beta_0$: 10.38 ± 1.28 (&lt;0.001)</td>
<td>-125.15</td>
<td>0.013 (NP)</td>
</tr>
<tr>
<td>$\alpha = 27.13$</td>
<td>WL: 1.22 ± 0.51 (0.021)</td>
<td></td>
<td>&lt; 0.001 (BM)</td>
</tr>
<tr>
<td>$\sigma^2 = 595.77$</td>
<td>AL: -0.07 ± 0.03 (0.011)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lambda</td>
<td>$\beta_0$: 10.16 ± 1.81 (&lt;0.001)</td>
<td>-127.09</td>
<td>0.134 (NP)</td>
</tr>
<tr>
<td>$\lambda = 0.44$ (0–0.87)</td>
<td>WL: 0.89 ± 0.52 (0.090)</td>
<td></td>
<td>&lt; 0.001 (BM)</td>
</tr>
<tr>
<td>$\sigma^2 = 58.89$</td>
<td>AL: -0.08 ± 0.03 (0.003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-phylogenetic (NP)</td>
<td>$\beta_0$: 10.54 ± 1.18 (&lt;0.001)</td>
<td>-128.21</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>WL: 1.34 ± 0.47 (&lt; 0.006)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>AL: -0.07 ± 0.02 (&lt; 0.005)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brownian motion (BM)</td>
<td>$\beta_0$: 9.42 ± 3.93 (0.021)</td>
<td>-133.57</td>
<td>-</td>
</tr>
<tr>
<td>$\sigma^2 = 275.45$</td>
<td>WL: 1.26 ± 0.51 (0.017)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>AL: -0.06 ± 0.03 (0.017)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

2. Heavier species have less efficient wing morphology for gliding
Wing loading was negatively correlated with aspect ratio (estimate: $-0.39 \pm 0.12$ SE, $R^2 = 0.18$, $p = 0.002$; Fig. 3), which is likely to reduce flight efficiency during gliding flight\(^4\).

**Discussion**

Variation in colouration among closely related species is not often easily explained, and there can be many competing hypotheses. One such hypothesis was proposed by Hassanalian et al.\(^{10}\), who found that a dark surface on the upper side of artificial wings reduces skin friction drag. Birds that spend a long time in flight, such as seabirds, could therefore be expected to benefit from dark wing pigmentation. Rogalla et al. corroborated this hypothesis and showed that darker birds’ wings do indeed create less drag when exposed to radiation\(^4\). However, because the production of melanin, the pigment responsible for dark feather colouration, is likely to be costly\(^7,16\), a trade-off can be expected. It is unlikely that species would produce dark feathers if the benefits they confer become superfluous. I proposed that species with a higher wing loading, which has a detrimental effect on flight efficiency, could be expected to have darker wings. Consistent with this expectation, mantle darkness in the Larinae varies widely but tends to be darker in species with higher wing loading, regardless of ancestry.

Furthermore, gull species with a higher wing loading have lower aspect ratio wings. High wing loading among birds is principally driven by a faster increase in mass than wing area as body size increases, a pattern observed across the avian class (excepting hummingbirds)\(^{17}\). As wing area reliably increases with increasing body mass\(^{17}\), a decrease in aspect ratio in gulls must occur as a result of wing breadth increasing faster than wing length. It therefore appears possible that darker mantles have evolved in gull species that have become heavier as a means of compensating for the reduction in flight efficiency that results from possessing wings that are relatively short both in proportion to body mass and to wing breadth.

Although the finding that higher wing loading is associated with darker mantles may appear to contradict the findings of Rogalla et al.\(^4\), in actuality both studies support the central hypothesis, which is that dark wing pigmentation increases flight efficiency. In some seabird taxa, such as albatrosses, species may use multiple means of optimizing flight efficiency, by decreasing wing loading and increasing both aspect ratio and melanin pigmentation. This may be because these species spend longer in flight than do gulls, and benefit from minimizing drag rather than optimizing maneuverability. While high aspect ratio wings cause a reduction in induced drag during flight, they are not optimal for take-off\(^{17}\). It is likely that gulls, which spend longer on land and at rest than most seabirds\(^{18}\), require wings optimized for rapid and regular take-off, which is a particular challenge for species with high wing loading.

Other factors besides those examined in this analysis will explain some of the variation in mantle darkness observed across the Larinae. The average length of foraging trips undertaken by each species could potentially influence this trait, as species that remain airborne for longer will have a greater need to optimize long distance flight rather than maneuverability during take-off. Migration distance may also be
a key factor. For example, Herring Gull (L. argentatus) and Lesser Black-backed Gull (L. fuscus) have similar wing loading and breed at similar latitudes, but the latter has a far darker mantle. Lesser black-backed gulls migrate further, spending the winter near the equator. Migration distance and absolute latitude are, however, likely to be highly correlated: species nearer the poles are more likely to be migratory and have longer migration distances. Lesser black-backed gulls and species with similar migration ecology may benefit from having darker plumage to protect their flight feathers from solar radiation, or perhaps because long distance migrants accrue greater benefits from reducing drag. These hypotheses are not mutually exclusive. Additionally, it is plausible that species nearer the equator gain more utility from dark pigmentation reducing drag owing to the greater insolation in these regions.

Differences in colouration between closely related species could also act as a means of species recognition, preventing or reducing potentially costly hybridization, or as a result of sexual selection for honest signals of mate condition. Hybridization is relatively common in gulls, yet there remain distinct phenotypes. Experimental studies would need to be conducted to assess whether plumage colour is an important marker of species identity and condition in gulls. The present study indicates that, at least in part, variation in colour has evolved for reasons other than selection pressures imposed by conspecific or heterospecific visual systems, as is the case in mate recognition and camouflage.

These results highlight the conditions under which colouration can function to increase fitness in ways that are unrelated to visual ecology. It is possible that colour may function in a similar, as yet undiscovered, way in other animal taxa. Furthermore, there may be potential for flight efficiency of aircraft to be improved by imitating the dark feather pigmentation that is widespread in seabirds.

**Methods**

1. Mantle darkness

I used the mantle darkness values provided in the supplementary material of Dufour et al. in their analysis of the relationship between gull mantle colouration and climactic conditions. They follow the Kodak grey scale (KGS) method of measuring gull mantle darkness, which has 20 units from 0 (white) to 19 (black), and calculated the mean values provided by Olsen and Howell and Dunn. I only considered full species (N = 51) according to Jetz et al.’s BirdTree in my analysis so, where measurements were provided for subspecies, I calculated the mean for the species. American Herring Gull (L. smithsonianus or L. argentatus smithsonianus) is treated as conspecific with European Herring Gull (L. argentatus).

2. Wing loading

Wing loading requires an estimate of wing area, which is not widely available in the literature. I therefore used the information on hand length (H, known as wing length) and first secondary feather length (S) provided by the AVONET database and calculated wing area with the following equation:
Wing area = (Wingspan – 2·H)·S + 2(H·S·0.5)

This method has been used in a study of common sandpipers (*Actitis hypoleucos*) and, while it underestimated wing area compared to planforms (drawings of the outline of a bird with the wings extended), the two measurements were significantly and highly correlated (R = 0.83, p < 0.01). I obtained wingspan measurements from Olson. As only ranges were provided, I took the central value. These were highly correlated with both the minimum and maximum wingspan (both R > 0.98). There was no wingspan measurement available for Relict Gull (*Ichthyaetus relictus*), and therefore this species was not included in the analysis. The final sample size was therefore 50. I divided the wing area calculation by the body mass (also from AVONET) to obtain the final estimate of wing loading. To aid interpretation of the regression coefficient, I standardized this variable such that the mean takes a value of 0.

3. Covariate: absolute latitude

AVONET also provides the centroid latitudes (the geometric centre) of the breeding and resident ranges for each species. I converted these to absolute values, termed “absolute latitude”, to obtain a variable to include as a covariate in the analysis. This variable denotes the distance from the equator in degrees and is a proxy for the amount of insolation experienced by each species.

4. Phylogenetic comparative analysis

To control for shared ancestry, I downloaded the maximum clade credibility tree of Lari from the supplementary material of Jetz et al. (2012) and pruned the tree to include only the Larinae. I used the package `phylolm` in R v. 4.1.2 to run phylogenetic generalized least squares regressions of the relationship between wing loading and mantle darkness with absolute latitude as a covariate. As there is some contention in the literature about which type of phylogenetic model should be used, I ran four different models for comparison (see Introduction). I compared the fit of the two models with fewer restrictions (NP and BM) with the two models with an extra parameter (OU and lambda) and selected the best supported model for inference while also reporting the results of the other models. In addition, to assess whether selection of the OU model over the BM model was not simply a result of bias in the tree, I simulated traits evolving along the tree through both a BM and an OU process 500 times and compared the difference in AIC in these simulations with the difference in AIC between the OU and BM model (see code provided).

The phylogenetic tree of the Larinae, with ancestral values of mantle darkness estimated along the branches, was produced using `contMap` in the package `phytools`.

5. Aspect ratio

The aspect ratio of each species was calculated by dividing the square of the wingspan by the wing area. I conducted a linear regression with aspect ratio as the dependent variable and standardized wing loading as the independent variable.
References


**Figures**
Figure 1

The evolution of mantle darkness in the Larinae and its relationship with wing loading and latitude.

Branches show the estimated ancestral states of mantle darkness, with the current, observed states at the tips. The approximate mantle darkness of each species on the Kodak grey scale (M) is also shown along with relative values of standardized wing loading (L) and absolute latitude (distance from the equator in degrees, E). The height of the phylogenetic tree is 0.21 million years. Note: genus names of the original BirdTree phylogeny have been amended to reflect current nomenclature.
Figure 2

Model estimates of the effect of wing loading and latitude on mantle darkness, measured on the Kodak Grey Scale (KGS). (a) Wing loading at 45 degrees from the equator; (b) absolute latitude (distance from the equator of species' breeding and resident ranges in degrees) at sample mean wing loading (0 SD). Predictions for Ornstein-Uhlenbeck (best-supported; solid line with standard error), non-phylogenetic (dotted line) and Brownian motion (dashed line) models of evolution are shown.
Figure 3

The relationship between wing loading and aspect ratio in the Larinae. Species that are heavier relative to their wing area have a relatively broader wing chord. The shaded area depicts standard error. N = 50.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Larinaeanalysiscode.txt
- larinae.txt