



SYMMETRY OF BLACK WINGTIPS IS RELATED TO CLUTCH SIZE AND INTEGUMENT COLORATION IN BLACK-LEGGED KITTIWAKES (*RISSA TRIDACTYLA*)

SARAH LECLAIRE,^{1,2,5} PIERRICK BLANCHARD,^{1,2} JOËL WHITE,^{1,2,3} SCOTT A HATCH,⁴
AND ÉTIENNE DANCHIN^{1,2}

¹CNRS, Université Paul Sabatier, ENFA; Laboratoire Évolution et Diversité Biologique (EDB), UMR5174, 118 route de Narbonne, 31062 Toulouse, France;

²Université Toulouse 3 Paul Sabatier, CNRS; EDB, UMR5174, 31062 Toulouse, France;

³Terrestrial Ecology Unit, University of Ghent, 9000 Ghent, Belgium; and

⁴U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA

ABSTRACT.—Fluctuating asymmetry has been suggested to be a phenotypic marker of developmental stability and is often seen as an indicator of overall quality. However, its role in sexual selection has been debated. To determine the potential role of black wingtip asymmetry in sexual selection in Black-legged Kittiwakes (*Rissa tridactyla*), we investigated whether symmetry was correlated with reproductive success and integument coloration, a trait probably sexually selected in this species. We found that, in males, asymmetry was associated with low clutch size and brood size but was independent of fledging success, which suggests that wingtip symmetry may reflect fertility in males. Asymmetry of black wingtip was also associated with duller integument, which emphasizes the potential importance of integument color in indicating individual quality. Further studies are needed to determine whether Black-legged Kittiwakes can discriminate between asymmetric and symmetric birds and use it as a cue in mate choice or intrasexual competition. Received 7 March 2013, accepted 5 June 2013.

Key words: asymmetry, integument coloration, kittiwakes, reproductive success, wingtips.

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RÉSUMÉ.—L'asymétrie fluctuante peut être le marqueur phénotypique d'une instabilité développementale, et est ainsi couramment considérée comme un indicateur de la qualité individuelle. Néanmoins, son importance dans la sélection sexuelle reste débattue. Afin de déterminer le rôle potentiel de l'asymétrie des taches alaires chez la mouette tridactyle (*Rissa tridactyla*), nous avons testé si cette asymétrie était corrélée au succès reproducteur et à la coloration des téguments, un trait probablement impliqué dans la sélection sexuelle chez cette espèce. Nous avons montré que l'asymétrie des taches alaires était associée à une faible taille de ponte et de nichée chez les mâles, mais n'était pas associée au nombre de jeunes à l'envol. L'asymétrie des taches alaires pourrait donc refléter le taux de fertilité chez les mâles. En outre, nous avons montré que l'asymétrie des taches alaires était corrélée à la couleur des téguments, soulignant ainsi l'importance de la couleur des téguments en tant qu'indice de la qualité individuelle chez cette espèce. D'autres études sont maintenant nécessaires pour déterminer si la mouette tridactyle peut discriminer des individus symétriques d'individus asymétriques, et utiliser cet indice lors du choix du partenaire ou dans la compétition intra-sexuelle.

DEVELOPMENTAL STABILITY REFLECTS the ability of individuals to undergo stable development under given environmental conditions (Møller 1997). Phenotypic measures of developmental instability include fluctuating asymmetry, which is defined as the unsigned difference between the two sides of a bilaterally symmetric morphological trait (Van Valen 1962). Fluctuating asymmetry may result from inbreeding (Clarke et al. 1986, Leamy and Klingenberg 2005, Lovatt and Hoelzel 2011, Vangestel et al. 2011), or adverse environmental conditions during development, such as high temperature, food shortage, chemical pollution, parasitism, and habitat disturbances (Clarke 1993, Møller 1996, Eeva et al. 2000, Brown and Brown 2002, Goodenough et al. 2008).

Therefore, fluctuating asymmetry is often seen as an indicator of overall quality or general health of individuals (Møller and Hoglund 1991; Møller 1997, 1999) and has been suggested to be a potential secondary sexual cue used by individuals during mate choice (Møller and Pomiankowski 1993, Møller and Thornhill 1998, Uetz and Smith 1999, Brown et al. 2008). Accordingly, in Zebra Finches (*Taeniopygia guttata*) and Swordtail Fish (*Xiphophorus cortezi*), females prefer males that have symmetric pigment pattern (Swaddle and Cuthill 1994, Morris 1998); and in humans, women prefer men with symmetric body shape (Brown et al. 2008). However, the generality of fluctuating asymmetry as a measure of developmental stability and predictor of fitness is still

³E-mail: sarah.leclaire@free.fr

being debated (Leung and Forbes 1996, Clarke 1998, Palmer 2000, Lens et al. 2002). The controversy stems, in part, from inconsistency across studies in fitness correlates and from a reporting bias in the literature. There is currently no consensus on the informativeness of fluctuating asymmetry, and accumulation of replicable results from investigations of a range of systems is needed.

In birds, fluctuating asymmetry of feather length and feather color pattern is common and develops during molt. Fluctuating asymmetry of feathers has therefore been shown to be an indicator of stress at the time of molt rather than during the embryonic or nestling period (Swaddle and Witter 1994, McGraw et al. 2002). Like many gull species, Black-legged Kittiwakes (*Rissa tridactyla*; hereafter “kittiwakes”) have black tips at the ends of their outer primary wing feathers. In some individuals, the black tips on P5 or P6 may differ from the normal symmetric pattern. Because P5 and P6 black tips are usually surrounded by white areas (Chardine 2002), they are clearly distinguishable during flight and rest (Fig. S1 in online Supplemental Material; see Acknowledgments). The general aim of our study is therefore to assess the fitness-signaling potential of wingtip asymmetry in kittiwakes.

The kittiwake is a genetically monogamous bird with a slight sexual size dimorphism (Jodice et al. 2000) and quasi-similar parental behavior between sexes (Leclaire et al. 2010). Although kittiwakes are strictly monogamous over a breeding season (Helfenstein et al. 2004), mate switching occurs in 19–47% of pairs each year (Coulson and Thomas 1983, Naves et al. 2006). As suggested for species with biparental care (Trivers 1972), mate choice should be mutual in kittiwakes, and cues that reliably indicate individual quality could thus be used for mate choice in both sexes. We therefore hypothesized that symmetry of black wingtips may indicate individual quality in males and females. First, we investigated whether wingtip symmetry was positively correlated with reproductive success. We then investigated whether breeding pairs showed assortative mating in relation to asymmetry, as would be expected if symmetric males and females are preferred by the other sex. Finally, we investigated whether wingtip symmetry was correlated with integument coloration, a trait that is probably sexually selected in this species (Leclaire et al. 2011a, b). A positive association is expected because both integument color and wingtip symmetry are thought to be a function of individual quality.

METHODS

Study site.—Our study was conducted from the beginning of May to mid-August 2007, 2009, and 2010 on a population of kittiwakes nesting on an abandoned U.S. Air Force radar tower on Middleton Island, Gulf of Alaska. Artificial nest sites created on the upper walls could be observed from inside the tower through sliding one-way windows (Gill and Hatch 2002). This enabled us to capture and monitor the breeders and their chicks. In all years, nest sites were checked twice daily, at 0900 and 1700 hours, to record events such as laying, hatching, fledging, or chick mortality. Laying, hatching, and fledging success were measured as the number of eggs laid (clutch size), the number of eggs hatched (brood size), and the number of chicks fledged, respectively. Only birds that laid eggs were monitored. Each bird was individually marked with a code of color rings for visual identification.

Symmetry.—At capture, photographs of both wings of 90 breeders in 2007, 243 breeders in 2009, and 244 breeders in 2010 were taken at a shooting distance of ~40 cm using a digital camera with flash and zoom. Fluctuating asymmetry is commonly defined as the difference between the value of the trait on the right side of the body minus that on the left (Van Valen 1962). However, we did not include a size standard in the pictures and, therefore, we could not measure a continuous value of asymmetry. Asymmetry was thus coded by examining the photos visually. It was coded as zero if black tips on the left and right wings were similar (Fig. S2 in online Supplemental Material), and as 1 if black tips were not identical in occurrence (82% of asymmetric birds; Fig. S3A in online Supplemental Material) or size (18% of asymmetric birds; Fig. S3B). Birds for which symmetry was uncertain (e.g., because of very small differences in tip size, or because of dirty or damaged feathers) were removed from the analyses. To confirm our categorization based on the size of the black tips, we compared the difference in black tip areas between the right and left wings in all birds classified as asymmetric because of a difference in black tip size, with the difference in 15 symmetric birds. Black tip area was measured with GIMP software (see Acknowledgments) by counting the number of pixels within it. The white paper label indicating the bird's identity and date, put next to the bird in each picture, was similar in the two photos of the same individual (Figs. S2 and S3A) and was therefore used as a size standard. To correct for bias due to zoom or shooting distance between pictures of the left and right wings, each black tip area was divided by the number of pixels in the size standard. Black wingtips of birds classified as asymmetric were more dissimilar in size than black wingtips of birds classified as symmetric (Mann-Whitney test: $W = 10$, $P < 0.0001$; mean \pm SE = 3.8 ± 0.1 times larger vs. 1.3 ± 0.0 times larger). Furthermore, 15 birds, captured twice within the same year, were always classified in the same symmetry category, thus confirming our symmetry categorization. All pictures were analyzed by S.L., who had no knowledge of the birds' characteristics during analyses.

In 2010, ten birds were captured during the late chick-rearing period (i.e., 9 August), 5 of which were clearly molting P5. Birds captured during the chick-rearing period were thus excluded from the statistical analyses, because kittiwakes may have already started molting their primaries in that period, and feathers may be relatively quite abraded, making the assessment of symmetry unreliable. Forty-five birds were captured both in 2007 and 2009, and 150 birds were captured both in 2009 and 2010.

Integument coloration.—In 2010, we measured gape, bill, and eye-ring colors on birds captured before laying. Gape and bill colors were measured with a reflectance spectrometer (USB2000; Ocean Optics, Dunedin, Florida), a deuterium-halogen light source (DH2000, Top Sensor System), and a 200- μ m fiber optic reflectance probe held at 45° to the integument surface. Reflectance was measured using SPECTRASUITE software (Ocean Optics) and in relation to a dark and a white standard (Spectralon, Labsphere, North Sutton, New Hampshire). The spectrometer was recalibrated after each measurement. We measured gape color at the intersection between the upper and lower mandibles, and bill color under the nostril on the upper mandible. We used two physical measurements: yellow chroma ([R700 nm – R450 nm]/R700 nm) and mean brightness (R300 – 700 nm), measured from the reflectance spectra using AVICOL software (see Acknowledgments). In numerous birds, including kittiwakes,

high yellow-chroma and low brightness are associated with higher carotenoid levels and more intense coloration (Giraudeau et al. 2011, Leclaire et al. 2011b).

Because light emitted by the spectrometer is dangerous for the birds' eyes, eye-ring color was measured from digital photographs. Pictures were taken at a standard distance of ~40 cm using a digital camera with flash. For each photograph, a color swatch was placed next to the bird to standardize measurements (Montgomerie 2006). All pictures were analyzed using Adobe PHOTOSHOP, version 7.0. For each picture, the average components of red, green, and blue (RGB system) were recorded within the whole area of the eye-ring. RGB components were then converted into saturation values, which represent color density (e.g., pink is less saturated than red).

All color measurements (gape and bill yellow-chroma, gape and bill brightness, and eye-ring saturation) were collapsed into a single score ($PC1_{\text{Color}}$) using a principal component analysis. $PC1_{\text{Color}}$ represented 37% of the variance and was positively related to gape and bill yellow-chroma (+0.46 and +0.49, respectively), and negatively related to gape and bill brightness (−0.59 and −0.40, respectively) and eye-ring saturation (−0.17).

Statistical analyses.—To test for a correlation between male and female reproductive success and wingtip asymmetry using a single model, one must include the pair identity as a random factor in the model, because reproductive success of males and of females are clearly not independent. However, such a model did not converge. We therefore studied the relationship between reproductive success and average asymmetry within pairs (zero when males and females were symmetric, 0.5 when only one member was asymmetric, and 1 when males and females were asymmetric). We used generalized linear mixed models (GLMMs) with reproductive success (clutch size, brood size, or fledging success) as the dependent variable, average asymmetry within pair as a fixed effect, and year as a random factor. We used a binomial distribution for the clutch-size analysis and a multinomial distribution for the brood-size and fledgling-number analyses. We used the same model to determine whether the relationship between pair asymmetry and reproductive success was driven mainly by males or by females, except that male asymmetry or female asymmetry was included as a fixed effect. Furthermore, because several birds were sampled in more than 1 year, bird identity was included as a random factor along with year to avoid pseudoreplication. Finally, we determined whether relative fledging success (i.e., proportion of young that fledged of young that hatched) was associated with male or female asymmetry using similar models.

Assortative mating was tested with a chi-square test, comparing the observed proportions of each category of pairs (i.e., pairs with two asymmetric individuals, pairs with one asymmetric and one symmetric individual, and pairs with two symmetric individuals) with the expected proportions under random mating. To determine whether asymmetry was correlated with integument coloration in 2010, we used an analysis of variance with $PC1_{\text{Color}}$ as the dependent variable and asymmetry, sex, and the interaction between sex and asymmetry as fixed effects.

All statistical tests were conducted with SAS, version 9.1 (SAS Institute, Cary, North Carolina). We used two-tailed Type 3 tests for fixed effects with significance level set at $\alpha = 0.05$. All GLMMs used the Satterthwaite correction for the calculation of

fixed-effects degrees of freedom (Littell et al. 2006). Values are expressed as means \pm SE throughout.

RESULTS

A total of 154 birds were asymmetric, of which 136 were asymmetric on P5, 17 were asymmetric on P6, and 1 was asymmetric on P4. There was no bias toward larger black tips or more black tips on the left or right side of the body ($\chi^2 = 2.29$, $P = 0.13$, and $\chi^2 = 0.82$, $P = 0.37$, respectively), which suggests that wingtip asymmetry is not directional. The proportion of symmetric birds did not differ between males and females (73.6% vs. 74.7%; $F = 0.07$, $df = 1$ and 472.2, $P = 0.80$), and asymmetry did not depend on the age of the birds ($F = 0.10$, $df = 1$ and 92, $P = 0.75$, $n = 74$ known-age birds).

Yearly changes.—The proportion of symmetric birds did not differ between years ($F = 0.93$, $df = 2$ and 485, $P = 0.40$). Intra-individual changes in wingtip patterns (i.e., differences in occurrence and/or tip size) between two consecutive years occurred in 56% of the birds, and intra-individual changes in symmetry category occurred in 29% of the birds. There was no consistent pattern in these changes. Some kittiwakes were symmetric first and then asymmetric in the following year, whereas others were asymmetric first and then symmetric in the following year. Similarly, some kittiwakes had larger tips in the first year, whereas others had larger tips in the second year. Repeatability of clutch size, brood size, and fledging success among individuals between years was low (intraclass correlation coefficients: 8%, 20%, and 13% respectively, in a GLMM with year as a fixed effect and individual as a random effect).

Symmetry in relation to assortative mating, reproductive success, and color.—There was no assortative mating in relation to symmetry of black wingtips ($\chi^2 = 3.92$, $P = 0.27$, $n = 201$ pairs). Males or females that laid early in the season were not more symmetric than birds that laid later in the season. Average asymmetry within pairs was associated with clutch size and tended to be associated with brood size ($F = 7.16$, $df = 1$ and 287, $P = 0.008$; and $F = 3.28$, $df = 1$ and 286, $P = 0.070$, respectively; Fig. 1). Pairs with higher average symmetry produced larger clutches and tended to have larger broods than pairs with lower average symmetry. However, average asymmetry within pairs was not related to fledging success ($F = 0.14$, $df = 1$ and 255, $P = 0.710$; Fig. 1). The correlations between average asymmetry within pairs and reproductive success were mainly driven by males. Males with symmetric wingtips had larger clutch and brood sizes than males with asymmetric wingtips ($F = 4.19$, $df = 1$ and 215, $P = 0.046$; and $F = 4.19$, $df = 1$ and 214, $P = 0.042$, respectively; Fig. 2A, B), but they had similar fledging success ($F = 0.02$, $df = 1$ and 162, $P = 0.90$; Fig. 2C). Symmetric and asymmetric females did not differ in clutch size, brood size, and fledging success ($F = 2.18$, $df = 1$ and 238, $P = 0.14$; $F = 0.27$, $df = 1$ and 237, $P = 0.60$; and $F = 0.01$, $df = 1$ and 190, $P = 0.94$, respectively; Fig. 3). Neither symmetric and asymmetric females nor symmetric and asymmetric males differed in relative fledging success (0.49 ± 0.04 vs. 0.46 ± 0.07 , $F = 0.10$, $df = 1$ and 125, $P = 0.75$; and 0.46 ± 0.05 vs. 0.55 ± 0.08 , $F = 0.81$, $df = 1$ and 112, $P = 0.37$, respectively). Within years, clutch size, brood size, and fledging success were correlated in the whole population (all $r > 0.4$, all $P < 0.001$, $n = 1,038$

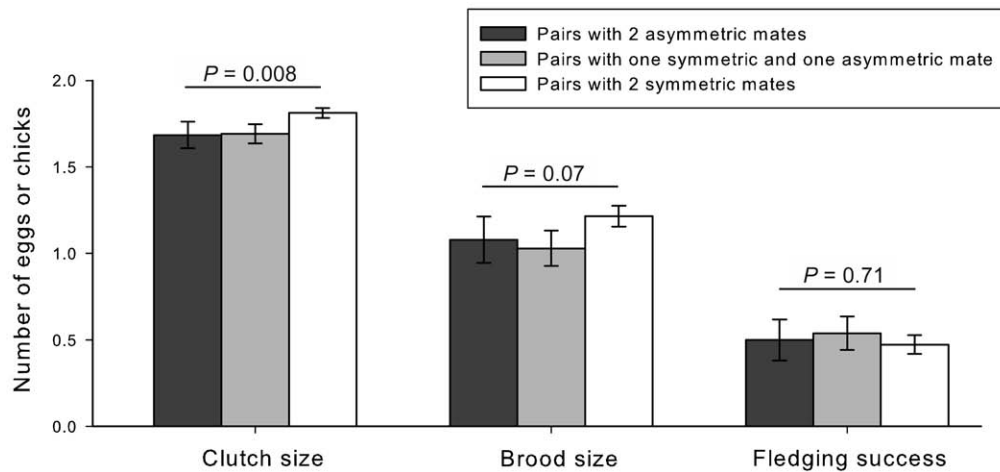


FIG. 1. Mean clutch size, brood size, and number of fledglings in Black-legged Kittiwake pairs in which the two mates had asymmetric wingtips, in which one mate was symmetric and the other was asymmetric, and in which the two mates were symmetric, during the 2007, 2009, and 2010 breeding seasons on Middleton Island, Alaska. Error bars represent standard errors.

reproductive events). Integument color, as described by $PC1_{Color}$, was positively associated with black wingtip symmetry ($F = 6.22$, $df = 1$ and 80 , $P = 0.015$; Fig. 4) and did not depend on sex or the interaction between wingtip symmetry and sex.

DISCUSSION

In Black-legged Kittiwakes, the pattern of black wingtips has been suggested to be consistent between years within individuals (Cadiou 1993) and to have a genetic basis because the amount of black differs between populations (Chardine 2002). Our results indicate, however, that this pattern, as well as its symmetry, is not always consistent between years. This suggests that black wingtip patterns in kittiwakes may also depend on environmental and physiological conditions at the time of molt.

Pairs in which both birds were symmetric produced larger clutch sizes than pairs with at least one asymmetric bird (Fig. 1). This result was driven mainly by males: asymmetric males had

lower clutch size and brood size than symmetric males, whereas there was no difference in reproductive success between symmetric and asymmetric females (Figs. 2 and 3). This finding contrasts with the lack of association found between symmetry of tail black spots and breeding parameters in both sexes of Lesser Gray Shrikes (*Lanius minor*; Krištín et al. 2007). However, although individual clutch size, brood size, and fledging success were correlated in the kittiwake population as a whole, symmetric birds did not have higher fledging success than asymmetric birds. Black wingtip symmetry develops during molt (August–October; González-Solís et al. 2011) and may, therefore, reflect condition at molt rather than current condition. The accumulation of stochastic events (independent of individual quality) during the breeding season may, thus, lead to a decrease in the relationship between symmetry and fledging success. In addition, symmetry may reflect fertility, but not parental effort. For instance, symmetry may be related to sperm quality, as in White-clawed Freshwater Crayfish (*Austropotamobius italicus*) and gazelles (*Gazella* spp.; Gomendio

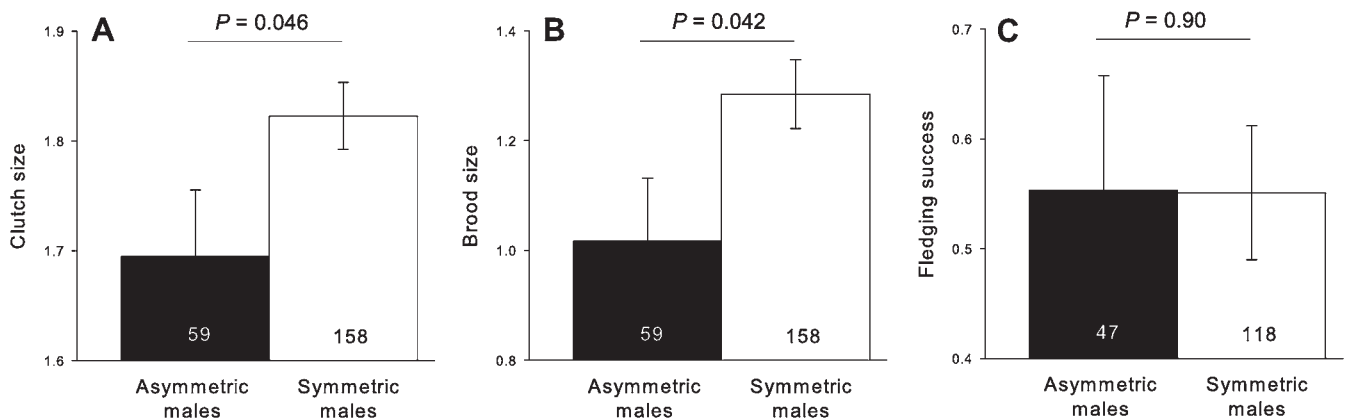


FIG. 2. (A) Mean clutch size, (B) brood size, and (C) number of fledglings in asymmetric and symmetric male Black-legged Kittiwakes in the 2007, 2009, and 2010 breeding seasons on Middleton Island, Alaska. Error bars represent standard errors and numbers within boxes are sample sizes.

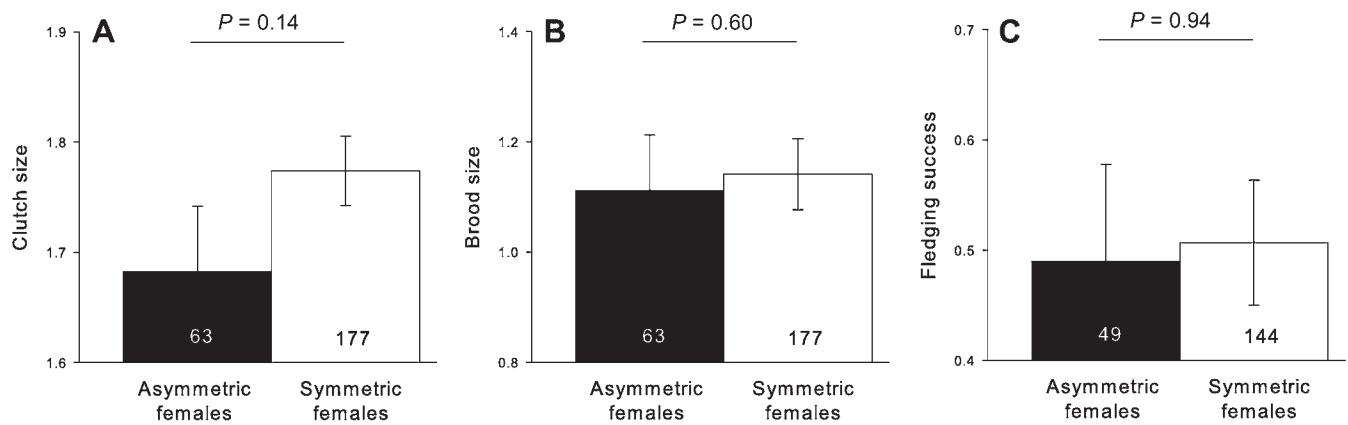


FIG. 3. (A) Mean clutch size, (B) brood size, and (C) number of fledglings in asymmetric and symmetric female Black-legged Kittiwakes in the 2007, 2009, and 2010 breeding seasons on Middleton Island, Alaska. Error bars represent standard errors and numbers within boxes are sample sizes.

et al. 2000, Galeotti et al. 2012), and may, therefore, be correlated with lower clutch size or higher hatching failures in asymmetric males. Hence, an asymmetric parent or its partner may compensate for lower brood size by investing more in parental care (Harris and Uller 2009). However, further studies on parental behavior are clearly needed to determine whether the lack of association between fledging success and wingtip asymmetry was due to parental care compensation.

We further found that more intensely colored birds were more symmetric than less intensely colored birds (Fig. 4). In many species, carotenoid-based colors are sexually selected traits (e.g., Hill 2006, Giraudeau et al. 2011). In accordance, previous studies in kittiwakes found that integument coloration was related to reproductive success in males and that experimentally

handicapped males were duller than controls, which suggests that integument coloration in kittiwakes may be ornaments (Leclaire et al. 2011a, b). A similar correlation between coloration and asymmetry in feathers was detected in Blue Tits (*Cyanistes caeruleus*; Galván 2011). Like Blue Tits, kittiwakes may therefore have the potential to perceive the developmental stability of conspecifics through the evaluation of integument color. This result emphasizes the potential importance of integument coloration as a sexual cue in kittiwakes. Whether kittiwakes can also directly detect wingtip symmetry of their conspecifics is unknown. The ability of birds to discriminate between small differences in symmetry has been debated. European Starlings (*Sturnus vulgaris*), for instance, are not able to accurately discriminate symmetry from asymmetry in a complex dot pattern that resembles their plumage (Swaddle and Ruff 2004). By contrast, experiments in Zebra Finches have shown that females prefer males with symmetric, as opposed to asymmetric, chest plumage (Swaddle and Cuthill 1994). Experimental manipulation of black wingtips is needed to determine whether kittiwakes can assess wingtip asymmetry and use this cue in mate choice by females or intrasexual competition in males.

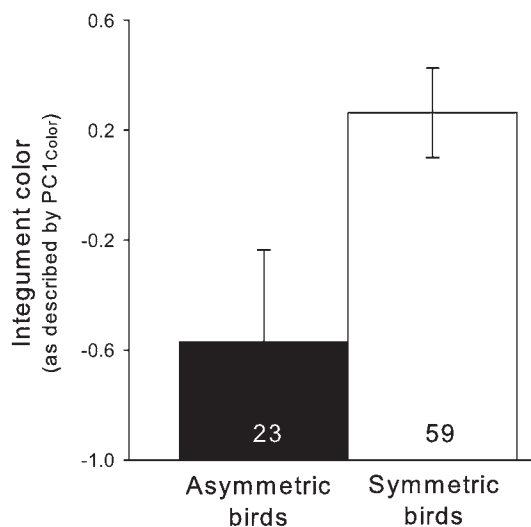


FIG. 4. Gape, bill, and eye-ring coloration as described by PC1_{Color} in asymmetric and symmetric Black-legged Kittiwakes breeding on Middleton Island, Alaska, in 2010. Error bars represent standard errors and numbers within boxes are sample sizes.

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**Supplementary
Online
material**



Supplementary Online Material for SYMMETRY OF BLACK WINGTIPS IS RELATED TO CLUTCH SIZE AND INTEGUMENT COLORATION IN BLACK-LEGGED KITTIWAKES (*RISSA TRIDACTYLA*)

SARAH LECLAIRE,^{1,2,5} PIERRICK BLANCHARD,^{1,2} JOËL WHITE,^{1,2,3} SCOTT A HATCH,⁴
AND ÉTIENNE DANCHIN^{1,2}

¹CNRS, Université Paul Sabatier, ENFA; Laboratoire Évolution et Diversité Biologique (EDB), UMR5174, 118 route de Narbonne, 31062 Toulouse, France;

²Université Toulouse 3 Paul Sabatier, CNRS; EDB, UMR5174, 31062 Toulouse, France;

³Terrestrial Ecology Unit, University of Ghent, 9000 Ghent, Belgium; and

⁴U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA

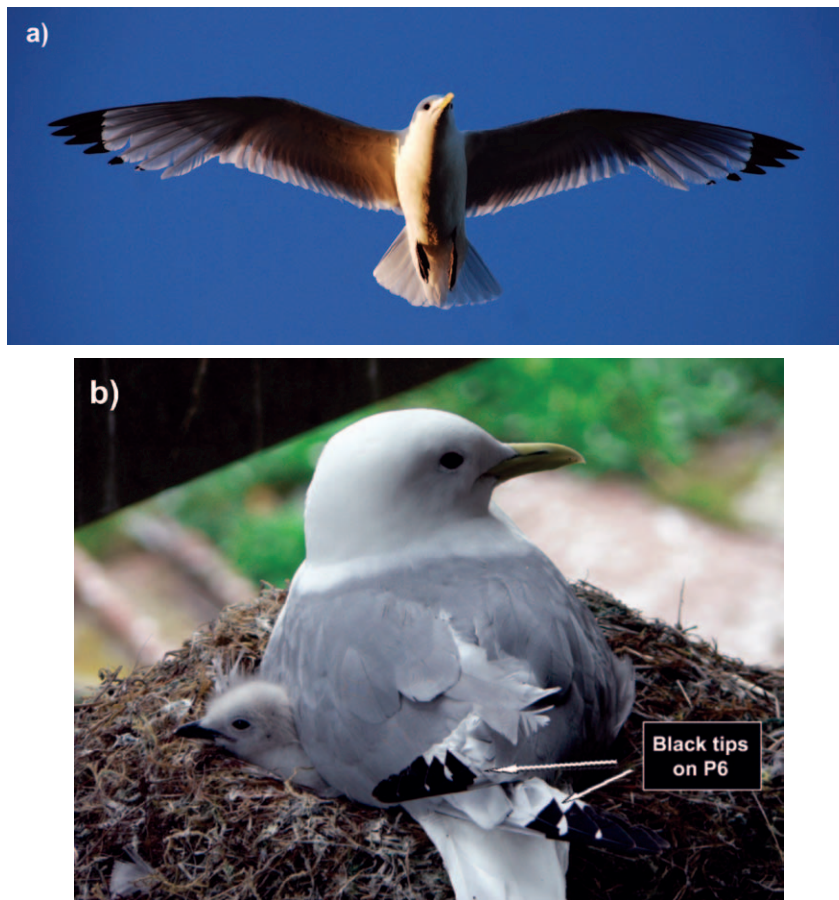


FIG. S1. Pictures showing that the P5 and P6 primary feathers are visible (A) when Black-legged Kittiwakes are flying (photograph by Emilie Moëc) and (B) when they are on the nest (photograph by Sarah Leclaire).

⁵E-mail: sarah.leclaire@free.fr

The following is supplementary to *The Auk*, Vol. 130, No. 3, pages 541–547.

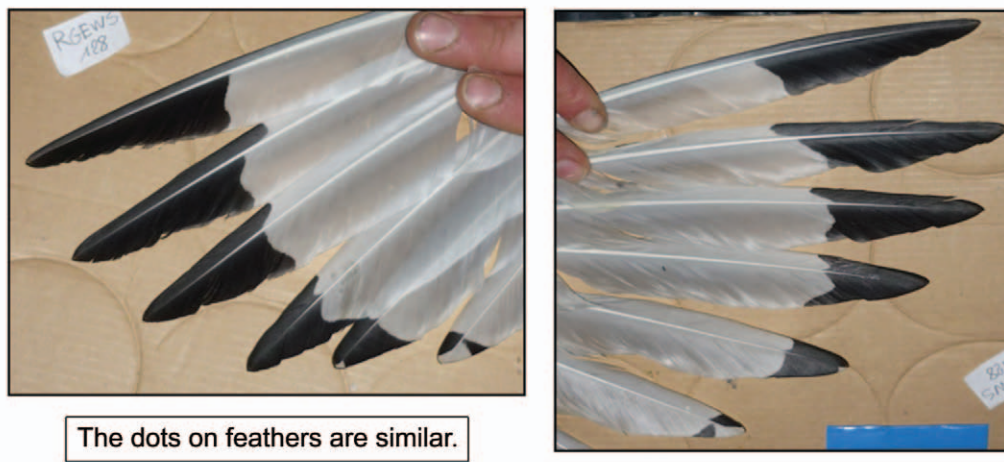


FIG. S2. Photographs of the two wings of a symmetric Black-legged Kittiwake.

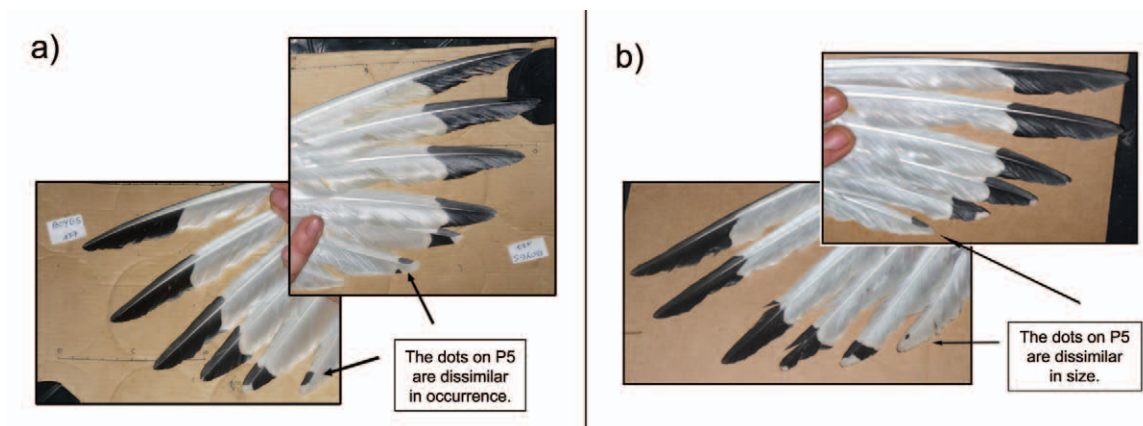


FIG. S3. Photographs of the two wings of an asymmetric Black-legged Kittiwake. Arrows show the two black tips that are not identical (A) in occurrence and (B) in size.