

Wing wear, but not asymmetry in wear, affects load-lifting capability in bumble bees *Bombus impatiens*

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Abstract: Wing wear is widespread in flying insects, but its effects on flight are controversial. In this research, we examine the separate and combined effects of wing area and wing area asymmetry on maximum load-lifting capability in bumble bees *Bombus impatiens* Cresson, 1863. Individual bees with experimentally induced forewing wear (0%–24% forewing area loss, 0%–38% forewing area asymmetry) were harnessed with a string to which small bead groups were attached and tested in a flight chamber to measure the maximum weight that they could lift incrementally. Wing wear significantly decreased load-lifting ability: the higher the mean wing area loss, the less mass a bee could lift (2.66 mg load reduction per 1% forewing area loss, which represents ~1.6% of mean body mass or ~5.2% of expected mean nectar load). However, wing area asymmetry, both alone and in combination with area loss, had no detectable effect on maximum lift. The clear cost of wing wear for bumble bees is a linear reduction in weight-lifting capability through loss of wing area. This relatively strong diminution of load lifting by wing wear, observed over the range of wing area losses naturally accrued by wild bees, provides a potential mechanism for declining foraging ability and survivorship of worker bees with wing wear. What remains to be explained is the utter insensitivity of maximum load lifted to forewing asymmetry.

Key words: area asymmetry, *Bombus impatiens*, bumble bee, insect flight, load lifting, wing wear.

Résumé : Si l'usure des ailes est répandue chez les insectes volants, ses effets sur le vol ne font pas l'unanimité. Nous examinons les effets séparés et combinés de la surface alaire et de l'asymétrie de cette dernière sur la capacité maximum de levage de charge chez les bourdons fébriles (*Bombus impatiens* Cresson, 1863). Des bourdons présentant une usure de l'aile antérieure d'origine expérimentale (réduction de 0 % à 24 % de la surface des ailes antérieures, asymétrie de 0 % à 38 % de cette surface) ont été harnachés avec un fil auquel des groupes de petites billes étaient attachés et ont fait l'objet d'essais en enceinte de vol visant à mesurer le poids maximum qu'ils pouvaient lever progressivement. L'usure des ailes causait une réduction significative de la capacité de levage de charge; plus la réduction moyenne de la surface alaire était grande, plus le poids pouvant être levé par un bourdon était faible (réduction de 2,66 mg de la charge pour une réduction de la surface alaire de 1 %, soit ~1,6 % de la masse corporelle moyenne ou ~5,2 % de la charge moyenne de nectar attendue). L'asymétrie de la surface alaire, seule ou combinée à la réduction de cette surface, n'avait toutefois aucun effet sensible sur la capacité de levage maximum. Le coût net de l'usure des ailes pour les bourdons fébriles est une réduction linéaire de la capacité de levage de charge découlant de la réduction de la surface alaire. Cette réduction relativement importante de la capacité de levage de charge découlant de l'usure des ailes, observée pour toute la fourchette de réduction naturelle de la surface alaire chez les bourdons à l'état sauvage, constitue un mécanisme qui pourrait expliquer la diminution de la capacité d'approvisionnement et de la survie des ouvrières associée à l'usure des ailes. Le fait que la charge maximum levée ne soit aucunement influencée par l'asymétrie des ailes antérieures demeure toutefois sans explication. [Traduit par la Rédaction]

Mots-clés : asymétrie de la surface, *Bombus impatiens*, bourdon fébrile, vol d'insecte, levage de charge, usure des ailes.

Introduction

The insect exoskeleton is formed from lightweight and mechanically efficient cuticle (Vincent and Wegst 2004), and clads members of the most ecologically and evolutionarily successful phylum (Mora et al. 2011). Cuticle is susceptible to wear, particularly in mechanically important structures like ovipositors (Lalonde and Mangel 1994), mandibles (Roitberg et al. 2005), leg segments (Morse 1981; Harwood et al. 2013), and wings (Mueller and Wolf-Mueller 1993). Such wear can impose significant ecological costs (e.g., Schofield et al. 2011).

The case of wear in insect flight structures is particularly interesting, in part because despite its ubiquity (such that its extent is routinely used to estimate age: Tyndale-Biscoe 1984; Mueller and Wolf-Mueller 1993), its overarching relevance to behaviour and physiology is controversial. Some research has found little or no

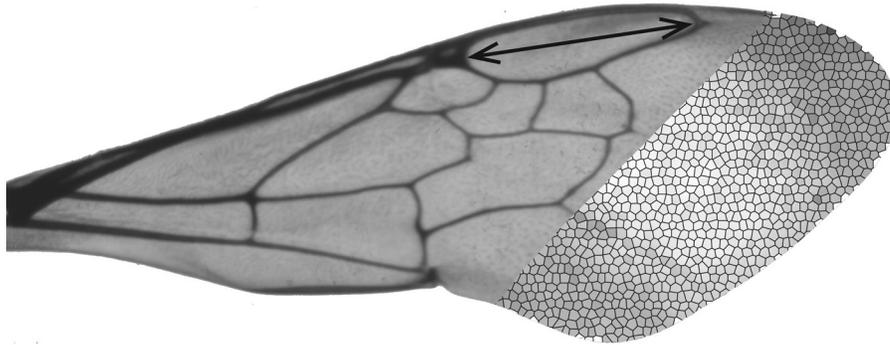
immediate cost of wing wear. Removing roughly 10% of the forewing area of worker buff-tailed bumble bees (*Bombus terrestris* (L., 1758)) had no detectable effect on their metabolic costs of flight, assessed during hovering flight in a small chamber (Hedenstrom et al. 2001). Removing up to 40% of the forewing area of worker bumble bees *Bombus flavifrons* Cresson, 1863 had minor effects on flight performance in bumble bees foraging in a simple environment (Haas and Cartar 2008). Western white butterflies (*Pontia occidentalis* (Reakirt, 1866)) whose wings were trimmed by 15%–20% survived as well in the field as did unclipped controls (Kingsolver 1999). In contrast, other research has found significant costs of wing area loss, in particular a ~40% increased rate of mortality in bumble bees *Bombus melanopygus* Nylander, 1848 (Cartar 1992) and a ~20% decreased rate of foraging gain in honey bees (*Apis mellifera* L., 1758) (Dukas and Dukas 2011). This disparity begs the

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Fig. 1. Sample wing from a worker bumble bee *Bombus impatiens* showing the region of wing clipping (textured) along the trailing edge of the forewing. Wing margins were removed in straight cuts, parallel to the base of the textured area. Length of the marginal cell is indicated by a black double-head arrow. The base of the wing shows a slight folding, which is an artifact.



question: is wing wear biomechanically relevant to flying insects in nature?

One way to resolve the controversy over the costs of wing wear is to experimentally manipulate potential performance costs of flight with worn wings. Recent advances in the measurement of lifting ability of flying insects (Dillon and Dudley 2004; Buchwald and Dudley 2010) provide a relevant tool for assessment of costs of wear. For social insect foragers, rate of food delivery to their colony is a key component of their colony productivity. Quantifying the impact of wing wear on load lifted by foragers could therefore be a critical way to relate wing wear to foraging load size, and therefore to contributions to colony-level success.

There are two ways that wing wear might affect load lifted. First, there is the simple loss of wing area, resulting in increasing wing loading and decreased flight performance (Fischer and Kutsch 2000; Combes et al. 2010). Second, there is the asymmetry in area between wings on each side. Any imbalance may make it difficult to transmit a symmetrical force from the wing muscles to wings when the wings on the more worn side meet less air resistance than those on the other, resulting in decreased flight performance (Thomas 1993; McLachlan 1997; Haas and Cartar 2008). An imbalance in wing size caused by asymmetry might also result in an imbalance of wing moments of inertia (Dudley 2002), where effective movement of wings might be problematic. Finally, area loss and area loss asymmetry may interact, such that area loss has a disproportionate effect on reduction in load lifting when associated with high asymmetry. This interaction has hitherto been untested, but we expect to see a disproportionate effect on load lifting when high wing wear is combined with high asymmetry.

In this paper, we quantify the separate and combined effects of area loss and asymmetry of area loss on the load-lifting ability of worker bumble bees *Bombus impatiens* Cresson, 1863, using the method of asymptotic load lifting (Chai et al. 1997; Dillon and Dudley 2004; Buchwald and Dudley 2010). If wing wear has no effect on load-lifting ability, bees with more wing wear or more asymmetry in wing wear should be able to lift similar weight to bees with pristine wings, when controlling for other variables such as individual body size. Buchwald and Dudley (2010) previously examined the effect of loss of the entire hind wing on lift using this method, but did not consider forewing wear or wear asymmetry. In this experiment, we used wing wear and asymmetry levels closer to those experienced by wild bees, with greater potential relevance to explaining bee foraging under natural conditions.

Materials and methods

Foragers from a colony of commercially-bred bumble bees *B. impatiens* (Biobest Canada Ltd., Leamington, Ontario, Canada) were used in trials over a 3-week period. Bees were assumed to be of similar age and all individuals selected had near-pristine levels of

initial wing wear. Sucrose solution was provided to the colony ad libitum. Pollen was provided in excess and added directly to the colony. Laboratory conditions (ambient temperature, humidity) were held constant during the experimental period. Each experimental trial used a haphazardly selected worker bee that was attempting to fly from the colony when the lid was raised.

Bees were placed in the freezer for ~14 min to induce torpor and facilitate wing clipping and attachment of the beaded string. Neither time spent in the freezer nor time spent recovering from freezing had a significant effect on load lifted when included in preliminary models. We used the asymptotic load-lifting method (Chai et al. 1997; Dillon and Dudley 2004; Buchwald and Dudley 2010; Mountcastle and Combes 2013) to measure load-lifting capacity of each subject. This method involves attaching a string adjacent to the center of mass of the subject, with beads serving as weights incrementally attached at a fixed interval along the string. A string of lightweight fishing line (Spiderwire EZ braid 0.18 mm; Spiderwire, Spirit Lake, Iowa, USA) ~22 cm long was attached using a noose knot to the bee's approximate center of mass: the petiole (Ellington 1984; Dudley and Ellington 1990). Beads were clustered into groups of 3; the first group was located between 4 and 5 cm from the bee, with each adjacent bead group separated by 2 cm of string. Bead groups weighed, on average, 15.34 mg (95% confidence interval (CI) = 15.18–15.50 mg, $n = 18$). Individual bees were observed taking off from the ground and sequentially lifting additional weights to some maximum height, which we associate with a maximum weight lifted. A priori treatment groups for wing loss and wing asymmetry were specified, ranging from 0% to 30% in both traits, in 10% increments. However, realized levels of wing loss and asymmetry differed from specified levels, and in the analyses we use realized levels. Treatments were applied randomly without replacement within nine temporally grouped blocks. Following attachment of the string to the bee, each wing was either clipped using dissecting scissors along the trailing edge of the forewing (to mimic natural wear) or left pristine (but with equivalent handling to the clipped bees), according to the prescribed treatment. For location of wing clipping see Fig. 1. Maximum wing wear was attained in a way such that wing veins were always left intact, to not compromise the structural stability of the wing. For asymmetry treatments, the wing receiving greater area loss (right vs. left) was determined randomly.

After clipping, bees were placed in a flight chamber similar to that used by Buchwald and Dudley (2010). When bees can fly several centimetres from the ground before lifting the first bead group, complications attributable to ground effects and commencement of flapping flight are reduced, and measurement of the force needed to overcome gravity is more straightforward (Dillon and Dudley 2004). The Plexiglas® chamber (20 cm × 30 cm × 20 cm high) was of sufficient size to avoid boundary or

ground effects (Rayner 1991) while the bee was lifting bead groups. A mirror was placed adjacent to one side of the chamber at a 45° angle and a video camera (JVC Everio G Series) was mounted 65 cm above the flight chamber to record all trials. The mirror allowed overhead and lateral views of the flight to be recorded simultaneously. A microphone (Sennheiser ME 66) was connected to the camera's audio input to record wingbeat frequency at the maximum flight capacity of each subject. Wingbeat frequency at maximum lift was quantified using Praat version 5.3.10 to determine the dominant pitch frequency. A 13 W compact fluorescent ultraviolet light (Blue Planet; Trileaf Distribution Trifeuil, Toronto, Ontario, Canada) was placed adjacent to the video camera and microphone above the flight chamber to stimulate flight (Jones and Buchmann 1974). After each subject was released into the flight chamber, flights were filmed (usually over 4–10 min) until flight performance began to deteriorate (determined by a decrease in flight attempts and a decrease in bead groups lifted). Bees that did not fly within 5 min in the chamber ($n = 9$) were deemed not capable of flight (see below) and were excluded from analysis. Of the bees that did fly, the mean number of flights was 20.8 (95% CI = 17.0–24.6 flights). Maximum height of each bee and thus maximum load lifted was determined by frame-by-frame examination of videos at a temporal resolution of 1/30 s (using SimpleMovieX version 3.11; Aero Quartet, SL, Sant Cugat del Valles, Spain). Only the highest lift was used in analysis for each subject, as we were interested in maximum performance of individuals (Dillon and Dudley 2004; Buchwald and Dudley 2010). Maximum load was obtained through examination of the maximum number of beads and string segments lifted. Load mass was estimated by cutting each string segment and bead group and weighing them individually.

Following each trial, bees were placed in plastic vials and frozen. Corpses were weighed within 15 days. Because bee honey crops were not emptied prior to evaluation of flight performance, we used two measures of body size: body mass and radial cell length (Fig. 1). To calculate wing area reduction and wing asymmetry, wing clippings and remaining wings of each bee were taped on paper and scanned at 600 dpi (dots per inch) using a Canon CanoScan LiDE 20 flatbed scanner. Wing area was calculated (in pixels) using Adobe Photoshop's (CS version 5.0) magnetic lasso function to extract forewings from the background. Percent wing loss asymmetry was calculated as

$$\% \text{ wing loss asymmetry} = \frac{|\text{area}_{L,\text{trimmed}} - \text{area}_{R,\text{trimmed}}|}{(\text{area}_{L,\text{trimmed}} + \text{area}_{R,\text{trimmed}})}$$

where L is left and R is right, and ranged from 0% to ~31% (Fig. 1). Percent area lost was calculated as

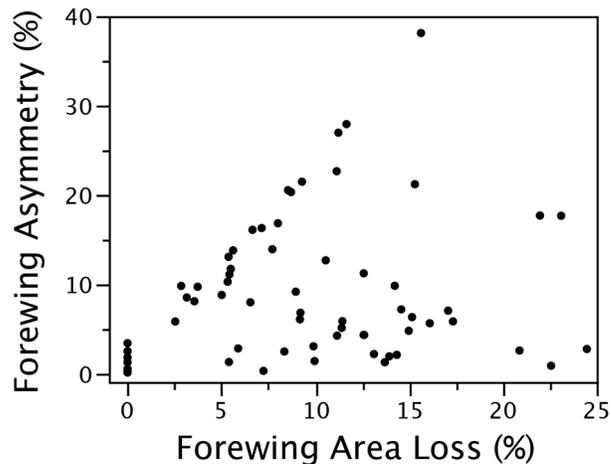
$$\% \text{ area loss} = \frac{[(\text{area}_{L,\text{pristine}} + \text{area}_{R,\text{pristine}}) - (\text{area}_{L,\text{trimmed}} + \text{area}_{R,\text{trimmed}})]}{(\text{area}_{L,\text{pristine}} + \text{area}_{R,\text{pristine}})}$$

where L is left and R is right, and ranged from 0% to ~25% (Fig. 1).

In Fig. 2, the nonzero asymmetry values for 10 bees with zero forewing area loss (i.e., both wings unclipped) reflect natural wing asymmetry, which for all bees averaged 1.4% (and for these unclipped bees averaged 1.1%). For similar reasons, we see some asymmetry values greater than 2× wing-loss values in Fig. 2.

We used a multiple regression to examine the individual and combined effects of wing area loss and asymmetry, and two measures of bee size (bee mass and marginal cell length) on maximum load lifted. We chose to use percent loss and body mass as independent variables, rather than wing loading, because this allows us to separate the individual and combined effects of wing area

Fig. 2. Realized covariation of mean forewing wear and asymmetry in experimental treatments imposed on worker bumble bees *Bombus impatiens* ($n = 66$).



and bee mass relative to area asymmetry. Wing loading is a ratio of wing area and mass, but with load mass included (and therefore producing a model with nonindependence of independent and dependent variables). Instead, we examine the partial effects of area and asymmetry after statistically controlling for mass and another measure of size (marginal cell length). Wingbeat frequency was initially included as a covariate but was dropped from the model, as it did not significantly explain load lifted and was not of a priori interest. We used a multiple regression to explain wingbeat frequency with the same dependent variables as described above, but present the final model retaining only the significant parameters. Temporal block (a fixed effect) was initially included in the model and then dropped for its lack of statistical significance to increase statistical power. All statistical analyses were performed using JMP version 9.0.2 (SAS Institute Inc., Cary, North Carolina, USA). Fitted models met the assumptions of homogeneity and normality of residuals, and variance inflation factors were all less than 2.

Results

A total of 74 worker *B. impatiens* were tested. Bee mass averaged 159.7 mg (SD = 19.1 mg, range = 121.1–205.8 mg). Bee forewing area averaged 26.43 mm² (SD = 1.50 mm², range = 21.58–32.12 mm²). Nine bees did not fly in our test chamber (i.e., they lifted no weight) and were excluded from the analysis, although their exclusion made no qualitative change to the results that we report here. These excluded bees were of intermediate wing area loss (11.3%, range = 6.4%–15.4%) and intermediate asymmetry (5.3%, range = 0%–16.2%), so their nonflight likely does not reflect extreme area loss or asymmetry. However, the excluded bees were smaller than average (mean = 141 mg, range = 124–184 mg), so their nonflight was likely either an artifact of handling or reflects an effect of their smaller size.

The regression model explaining maximum lift is presented in Table 1. Only mean wing wear and bee size (marginal cell length) explained lift (Fig. 3). Neither asymmetry nor bee mass had an effect on lifting ability (Fig. 3). Asymmetry and mean wing wear did not interact to explain maximum lift (Table 1). Maximum lift ability declined linearly with increases in mean wing loss (Fig. 3). The mean maximum lift for a 162 mg bee with unworn wings (i.e., the y intercept) is 62.1 mg (95% CI = 52.1–72.0 mg). Two separate analyses were performed on the data in the partial regression plot involving wing area (Fig. 3, top left). First, removal of the three highest values had no qualitative effect on the conclusion: their removal increased the slope by 3%. Second, we tested whether the

Table 1. Regression model predicting maximum load lifted (mg) by worker bumble bees *Bombus impatiens* from wing treatment and body-size metrics ($R^2 = 0.457$, $n = 66$).

Term	Estimate	P	95% Confidence interval		Standardized β
			Lower	Upper	
Intercept	-148.947	0.005	-250.793	-47.101	0.000
Forewing area loss (%)	-2.655	<0.0001	-3.582	-1.729	-0.643
Forewing asymmetry (%)	-0.192	0.593	-0.908	0.523	-0.059
(Area loss (%) - 9.24) \times (asymmetry (%) - 8.57)	-0.022	0.711	-0.141	0.097	-0.041
Body mass (mg)	-0.076	0.647	-0.405	0.254	-0.052
Mean marginal cell length (mm)	88.015	0.0003	42.387	133.643	0.437

Fig. 3. Partial regression plots showing the effects of forewing wear ("area loss"), forewing asymmetry, marginal cell length, and bee mass on maximum load lifted by worker bumble bees *Bombus impatiens* ($n = 66$), visualizing the multiple regression reported in Table 1. Variables are set at their mean values (area loss = 9.2%, asymmetry = 8.6%, marginal cell length = 2.6 mm, body mass = 162 mg). Figure appears in colour on the Web.

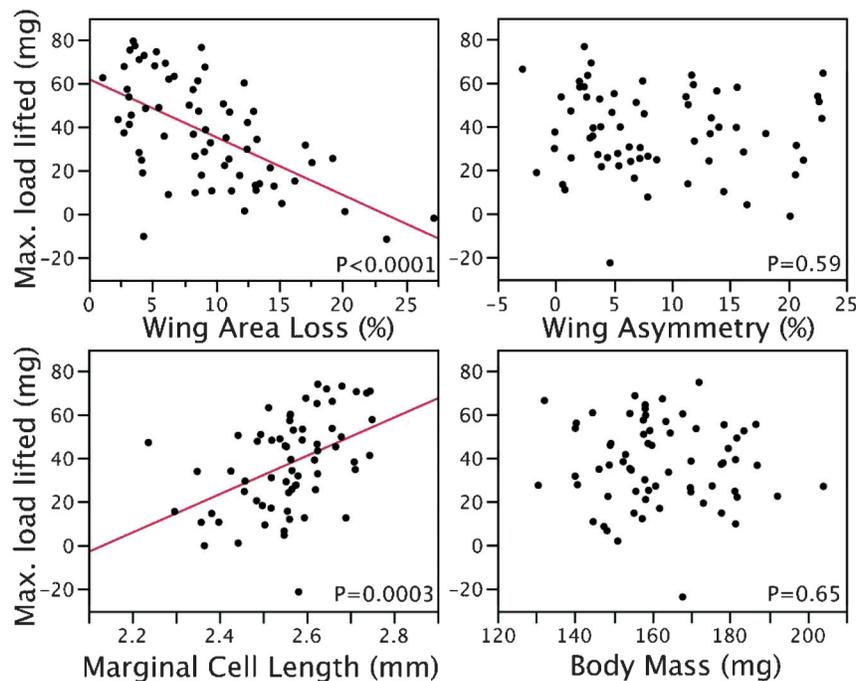
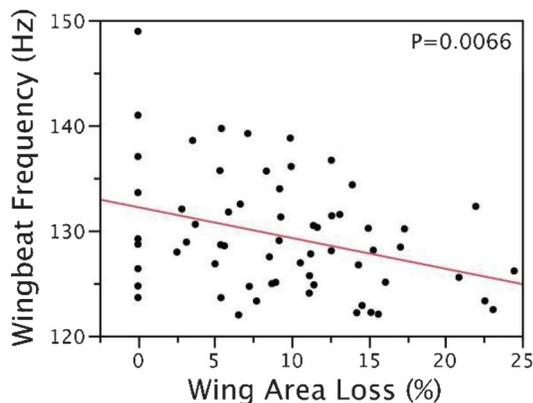


Fig. 4. Wingbeat frequency decreases with wing increased forewing wear in bumble bees *Bombus impatiens* (least-squares regression, $R^2 = 0.114$, $F_{[1,61]} = 7.91$, $P = 0.0066$, standardized $\beta = -0.339$). Figure appears in colour on the Web.



trend is only linear or if it has a nonlinear component: a linear model best explained the trend depicted in the wing area loss; a wear² term in a polynomial regression was not significant ($t_{[63]} = 0.12$, $P = 0.91$)

Maximum lift was strongly reduced by loss of wing area in flying worker bumble bees. For an average-sized bumble bee (162 mg), each percent increase in loss of forewing area (i.e., $\sim 0.27 \text{ mm}^2$) resulted in the loss of 2.66 mg of load-lifting capability (95% CI = 1.73–3.58 mg). For this average-sized bee, a 1% loss of wing area represents a loss of load-lifting capacity of $\sim 1.6\%$ (95% CI = 1.07%–2.20%) or $\sim 5.2\%$ (95% CI = 3.4%–7.0%) of the 51 mg nectar load of a 162 mg bumble bee under field conditions (R.V. Cartar, unpublished data). Hence, a bee with forewing wear of $\sim 25.5\%$ (95% CI = 10.9%–60.7%) of original wing area is expected to be unable to transport a nectar load of any size back to the colony.

Wingbeat frequency was negatively related to mean wing area loss (Fig. 4), but showed no relationship with asymmetry alone ($t_{[63]} = -0.08$, $P = 0.82$) or in interaction ($t_{[63]} = -0.69$, $P = 0.49$), or with body mass ($t_{[63]} = -0.55$, $P = 0.58$). An individual's wingbeat frequency did not change within a trial, so the negative relationship with wing area is unlikely to reflect an element of within-trial fatigue (analysis not shown).

Discussion

The strong reduction in load-lifting ability resulting from wing area loss should have a major effect on foraging ability. In honey bees, wing wear has been related to a decreased profitability of foraging trips (Dukas and Dukas 2011; Higginson et al. 2011) and

decreased choosiness of worker honey bees (Higginson and Barnard 2004), which likely results in lower wing use, since less choosy bees would be more likely to fly to closer inflorescences. Cartar (1992) found that bees with a large amount of wing wear stopped foraging. These alterations in foraging behaviour can be rationalized by our results: increased wing wear reduces a bee's ability to lift (nectar and pollen) loads. Wing wear also affects wing use in foraging bumble bees: bees with worn wings spent less time in flight and flew less often (Foster and Cartar 2011b).

Wing asymmetry has been found to detrimentally affect flight performance (McLachlan 1997; Haas and Cartar 2008) and ability to avoid predation (Møller 1996), and increases metabolic rate and flight wingbeat frequency (Hambly et al. 2004; Skandalis and Darveau 2012). Remarkably, wing asymmetry had no detectable effect on load-lifting ability in our study, either alone or in interaction with wing area. Bee load-lifting capacity appears to be extraordinarily robust to asymmetry, over a broad range of asymmetries (0%–38%). Why might asymmetry matter so little? Presumably, bees can better compensate behaviourally for increased wing asymmetry than for decreased wing area.

There are several potential mechanisms for bees to successfully compensate for wing asymmetry. First, symmetric lift production could be restored using asymmetric changes to wing-stroke amplitude, as was found when asymmetry was experimentally imposed on the wings of Zebra Finches (*Taeniopygia guttata* (Vieillot, 1817)) (Hambly et al. 2004) and hawkmoths (*Manduca sexta* (L., 1763)) (Fernández et al. 2012). Second, bees might couple a change in posture (by rolling the torso to favour the lower-area wing) with an increase wingbeat amplitude and (or) frequency (Dudley 1995; Altshuler et al. 2005), or an increase in angle of attack of the wings. Independent of these mechanisms, bees might also increase the muscular force delivered with each stroke (Skandalis and Darveau 2012). Most of these details are unavailable to us for our bees, but we did measure wingbeat frequency.

Worn wings should generate less lift with each beat, but increased wing loading from wing wear might easily be compensated for by increased wingbeat frequency (e.g., Cooper 1993; Kingsolver 1999). This adjustment of wingbeat frequency could allow for uncompromised load lifting over a broad range of wing area losses, should lift compensation be effective. Our wingbeat frequencies (mean = 130 Hz, range = 122–167 Hz) were lower than recently reported values for similar-sized bees, centering around ~180 Hz (Hedenstrom et al. 2001; Buchwald and Dudley 2010). However, our values seem consistent with lower *Bombus* spp. averages (range = 90–156 Hz) reported in older work (Greenewalt 1962; Byrne et al. 1988). We are perplexed by the difference, because a fundamental pitch frequency that we identified in this study cannot have lower harmonics. We speculate that the discrepancy between our values and recently published values may be an artifact of our flight chamber or measurement technique. Williams and Galambos (1950) found that wingbeat frequency (determined from fundamental pitch frequencies, as we did) varied widely depending upon the orientation of the insect with respect to the microphone. However, as our lower frequency values are consistent across individuals, the directional effect of wing area loss on wingbeat frequency that we report remains of interest.

And that effect of interest is surprising: wingbeat frequency significantly decreased with increasing wing wear. This result differs from numerous studies that have found that wing wear increases wingbeat frequency (e.g., Sotavalta 1952; Hargrove 1975; Cooper 1993; Kingsolver 1999; Hedenstrom et al. 2001; Foster and Cartar 2011a). However, there are some exceptions to this pattern. Honey bees decreased wingbeat frequency with age (Vance 2009), and frequency at maximum load-bearing capacity decreased with increases in body mass of Euglossine bees (Dillon and Dudley 2004). Buchwald and Dudley (2010) found decreased wingbeat frequency with removal of hind wings and attributed it to impairment of wing activation arising from a decrease in effective wing

area. When both wingbeat frequency and wing area are lower, the remaining behavioural adjustments (increased amplitude, power per stroke, and angle of attack) required for successful flight must perforce be more extreme. It is unclear why our bumble bees did not respond in the typical manner to loss of wing area (i.e., increase wingbeat frequency), and we speculate that this might be seen under maximum load lifting that is not seen lifting lighter loads. The relationship between load lifted and wingbeat frequency across a range of load sizes merits further study.

We expected larger bees to be capable of lifting larger loads, and this expectation was met for marginal cell length but not for body mass. Similarly, body mass did not explain maximum load lifted in bees (body mass specific vertical force production of Euglossine bees in Dillon and Dudley 2004; our regression using data from Table S1 of bumble bees in Buchwald and Dudley 2010). In contrast, other studies have found that foraging load increases with body size (e.g., Goulson et al. 2002). In our case, marginal cell length is likely a better measure of body size than body mass, because our measure of body mass is potentially confounded by (unmeasured) crop load. So our conclusion is that larger bees lifted larger loads.

Overall, loss of wing area translated linearly and with large effect size into a loss of load-carrying capacity, establishing a definitive cost of flying with wing wear. However, bees were remarkably resilient to variation in wing asymmetry. This suggests some kind of compensation mechanism for asymmetry in bumble bees that merits further study. Based on the wing area effect, a decrease in nectar-load efficiency (Higginson et al. 2011) and choosiness of flower quality and density (Higginson and Barnard 2004; Foster and Cartar 2011b) may be linked to the reduction in load-carrying capacity of foragers with wing wear. This link between maximum load-lifting capacity and wing wear may also extend to survival, should foraging bees have a compromised flight capacity (potentially arising from decreased maneuverability). Further experiments investigating predator avoidance and maneuverability of workers with worn and asymmetric wings while carrying nectar and pollen should illuminate the contribution of each of these factors to declines in foraging performance, and possibly to increased mortality, in bumble bees.

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