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Coping with nonrepairable body damage: effects of wing damage on foraging performance in bees

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Nonrepairable body damage such as tooth and wing wear commonly occur in animals and can dramatically alter their behaviour. We critically examined the effects of nonrepairable damage in a model system that enabled us to separate the effects of damage from other correlated effects of senescence. Compared to sham controls, honeybees with 20% of their front wings trimmed continued to forage at similar rates and reduced their net rate of food delivery by approximately 20%. The changes in flight behaviour allowing the foragers to cope with the substantial wing damage probably occurred immediately following wing trimming. Bees showed no increase in foraging performance either in successive trips or during the 2 days following wing trimming. The cost of maintaining relatively high foraging performance after sustaining severe wing damage was approximately a 20% increase in mortality rate, most likely owing to predation. Our results illustrate a remarkable versatility of honeybees' flight behaviour, which allows them to handle the inevitable nonrepairable body damage that naturally occurs with ageing.

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Most animals experience a cumulative increase in the probability of possessing nonrepairable body damage with age. Examples include tooth wear in mammals, claw damage in crabs and wing wear in insects (e.g. Juanes & Hartwick 1990; Mueller & Wolf-Mueller 1993; Kojola et al. 1998). Several studies have examined the effects of nonrepairable body damage on behaviour and fitness. In mammals, domestic goats (*Capra aegagrus hircus*) with severe tooth damage avoid grasses and consume more soft-leaved shrubs (Mellado et al. 2005), and female lemurs (*Propithecus edwardsi*) with more tooth wear suffer higher mortality of their infants when food is scarce (King et al. 2005). In crabs (*Cancer magister*), claw damage increases prey handling times and biases food preference towards smaller items (Juanes & Hartwick 1990). Generally, limb loss in several decapod crustaceans decreases feeding efficiency, growth rate and mating success (Juanes & Smith 1995).

In insects, a few studies examined the effects of wing damage on flight performance under controlled settings. In bumblebees, reduced wing area resulted in increased wing beat frequency but not in metabolic flight costs in *Bombus terrestris* (Hedenstrom et al. 2001),

and resulted in less direct flight paths between flowers in *B. flavifrons* (Haas & Cartar 2008). In dragonflies, wing trimming lowered vertical acceleration and average flight velocity in *Sympetrum rubicundulum* and reduced prey capture rates in *S. vicinum* (Combes et al. 2010). Field work documented that wing damage reduced honeybees' (*Apis mellifera*) tendency to reject low-quality flowers (Higginson & Barnard 2004), shortened the time spent in flight between flowers in six bumblebee species (Foster & Cartar, in press) and increased mortality rates in bumblebees (*B. melanopygus*) (Cartar 1992).

The above studies agree with the intuitive prediction that wing wear should reduce insect foraging performance. It is possible, however, that insects can adjust their behaviour with experience after suffering wing damage. In honeybees, the focus of our research, one can readily conceive of a few ways in which foragers could cope with wing wear. First, bees may undergo physiological changes allowing them to compensate for the increase in wing loading. Indeed, physiological research on honeybees indicates that, prior to becoming foragers, workers go through dramatic changes that increase their flight performance (Harrison 1986; Schippers et al. 2006, 2010; Vance et al. 2009). We know of no data pertaining to the physiological effects of increased wing loading owing to wing wear. In general, however, physiological adaptations to changing conditions have been well studied in a variety of taxa (Hochachka & Somero 2002). Second, bees could maintain a high foraging performance at the cost of expending

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more energy and reducing flight manoeuvrability, which could increase their mortality rate. Finally, bees could also cope with wing wear by decreasing their body weight to reduce wing loading. Such reductions in body weight occur during the regular worker transition from hive activity to foraging (Harrison 1986; Vance et al. 2009) and throughout a forager's life (Figure 2b in Dukas 2008c).

To evaluate the effects of wing damage on long-term foraging performance, we conducted a field experiment with honeybees. Honeybees are an excellent model system for studying the effects of nonrepairable body damage such as wing wear because of the relative ease of measuring their long-term foraging performance under natural and experimental settings (Dukas & Visscher 1994; Dukas 2008b, c). Specifically, we asked (1) how wing damage affects bees' net rate of food delivery and its components, (2) whether the net rate of food delivery by wing-damaged bees increases over time, (3) whether bees reduce their body weight following wing damage, (4) whether bees reduce the rate of their foraging trips following wing damage, and (5) whether wing damage reduces foragers' life span.

METHODS

We conducted the research at the Wildlife Research Station, Algonquin Provincial Park, Ontario, Canada in July–August 2010 using a protocol similar to the one described in Dukas (2008b). Briefly, we trained individually marked honeybees to visit a feeder providing 2.5 M sucrose water located 400 m from a two-frame observation hive. The hive was stationed inside a temperature-controlled research trailer and connected to the outdoors via a Plexiglas tunnel with a removable section, which we used for temporally trapping our focal bees and weighing them on an analytical balance with a precision of 0.1 mg. The balance reported bee weights directly to a computer and we added each bee's identity and her travel direction. We also recorded bees' departure and arrival times at the hive and feeder.

To control for daily variation caused by hive conditions and weather, our experiment involved matched pairs of bees that were always observed simultaneously. We chose only recently recruited bees with no wing damage and randomly assigned one bee to the wing trimming treatment and the other bee to the sham control. We recorded the bees' foraging performance for several trips as described above and in Dukas (2008b). We then captured the bees, chilled them on ice until they were immobilized, trimmed the distal parts of the two front wings of the treatment bees (as illustrated in Figure 1 of Hedenstrom et al. 2001) and touched the front wings of the control bees. Measurements of trimmed wings using ImageJ (National Institutes of Health, Bethesda, MD, U.S.A.) indicated that we removed $19.6 \pm 1.7\%$ (mean \pm SE, $N = 10$ bees) of the front wings. After handling, all the bees returned to the hive and later resumed foraging.

We divided our observations into four stages. Stages B and A1 occurred on day 1. Stage B consisted of the foraging trips before chilling, wing trimming and the matched sham control, while stage A1 included the trips immediately after the trimming and sham applications. Stages A2 and A3 comprised foraging trips on days 2 and 3, respectively. We had a total of 42 bees, half with trimmed wings and half matched controls, but the sample sizes became progressively smaller for the longer temporal scales owing to mortality. Note that we inferred mortality from the disappearance of bees, which is ecologically relevant because such bees no longer contribute to colony fitness. In each temporal scale, we included only matched pairs of bees, meaning that the death of one bee also eliminated her matched bee from the analyses of longer temporal scales. We included all 42 bees in the life span analyses, 38 matched bees for stages B and A1, 30 matched bees for stages B through A2 and 18 matched bees for stages B through A3. For each bee and stage, we attempted to have at least two departure weights, four arrival weights and four records of trip durations. To compare the rate of

visits following wing trimming and sham control, we recorded all visits by matched pairs for periods of 1–2 h and then calculated the hourly visit rate. For this data set, we had records for 13 pairs.

For conciseness, we focus on the net rate of food delivery from the feeder to the hive, calculated as the arrival minus departure weight of each bee over the trip duration from the feeder to the hive. Hence the net rate of food delivery has the units of milligrams per second. We present the detailed between-stage analyses for the 30 bees that survived through stage A2. We also present one long-term analysis for the 18 bees that survived through stage A3 and one short-term analysis of the foraging performance in the four trips immediately following the wing trimming and sham control for the 38 bees that survived through stage A1. The statistical analyses involved repeated measures ANOVAs examining the effects of treatment and experience within the matched pairs. Duration data were log transformed to meet ANOVA assumptions.

RESULTS

Long-term Performance

Following wing trimming, bees showed an $18.7 \pm 2.8\%$ decrease in the net rate of food delivery compared to a negligible decline ($2.2 \pm 2.3\%$) in the sham controls (repeated measures ANOVA: overall treatment by stage interaction: $F_{2,28} = 16.9$, $P < 0.001$; Fig. 1a). The wing-trimmed bees showed no increase in the net rate of food delivery compared to the controls from stage A1 to stage A2 (treatment by stage interaction: $F_{1,14} = 0.9$, $P = 0.35$; Fig. 1a). Separate analyses indicated that wing trimming caused both a decrease in the net weight of food delivered to the hive (treatment by stage interaction: $F_{2,28} = 4.6$, $P < 0.05$; Fig. 1b) and an increase in the trip duration from the feeder to the hive (treatment by stage interaction: $F_{2,28} = 9.4$, $P < 0.001$; Fig. 1c).

The analysis of the 18 matched bees surviving through stage A3 revealed a similar pattern of close to 20% decrease in the net rate of food delivery following wing trimming. The wing-trimmed bees showed a $17.4 \pm 4.7\%$ decrease in the net rate of food delivery compared to a negligible decline ($-0.1 \pm 3.3\%$) in the sham controls (treatment by stage interaction: $F_{3,25} = 4.3$, $P < 0.05$; Fig. 2) and no improvement from stages A1 through A3 (treatment by stage interaction: $F_{2,16} = 0.3$, $P = 0.7$; Fig. 2).

Short-term Performance

A trip-by-trip analysis of the performance of bees immediately following wing trimming and sham control indicated a steady difference of about 20% between the treatments ($F_{1,18} = 31$, $P < 0.001$; Fig. 3) with no short-term improvement in the net rate of food delivery in the wing-trimmed bees relative to the controls (treatment by trip interaction: $F_{3,51} = 0.2$, $P = 0.8$; Fig. 3).

Body Weight

Wing trimming was not associated with a decrease in the departure weight of bees compared to the controls (treatment by stage interaction: $F_{2,32} = 0.18$, $P = 0.17$). The wing-trimmed and control bees had similar departure weights ($F_{1,18} = 0.07$, $P = 0.8$) and both treatments reduced their departure weights over time (stage effect: $F_{2,38} = 15.2$, $P < 0.001$).

Rate of Foraging Trips

Wing-trimmed and sham control bees foraged at similar rates (7.4 ± 0.66 and 7 ± 0.65 trips/h, respectively; paired samples t test: $t_{12} = -0.8$, $P = 0.4$).

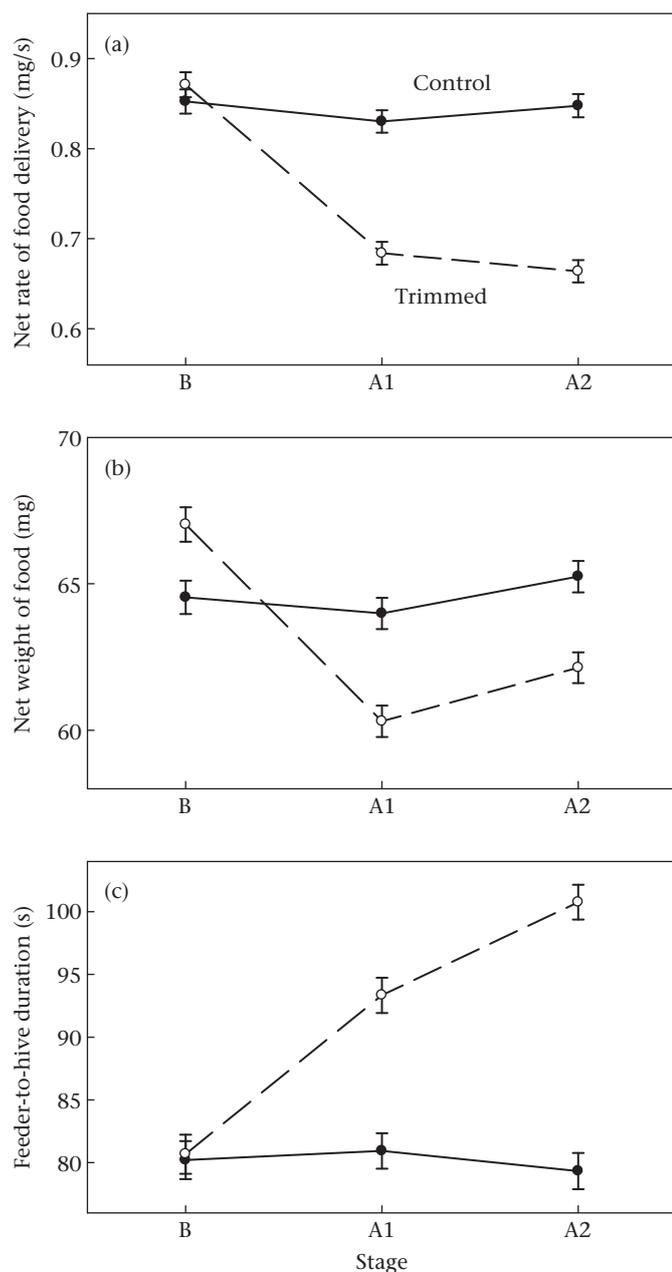


Figure 1. Average \pm SE (a) net rate of food delivery (mg/s), (b) net weight of food (mg) and (c) feeder-to-hive duration (s) before (stage B) and after (stage A1) wing trimming and sham control, and on the following day (stage A2) ($N = 30$ bees from 15 matched pairs).

Life Span

After the treatment, the life span of wing-trimmed bees was about 20% shorter than that of matched control bees (mean \pm SE life span: 3.7 ± 0.6 and 4.8 ± 0.5 days, respectively; paired samples t test: $t_{20} = 2.6$, $P < 0.05$).

DISCUSSION

Honeybees coped well with the loss of about 20% of their front wing area. The wing damage did not alter the bees' rate of foraging trips but caused approximately a 20% decrease in the net rate of food delivery (Fig. 1). Much of the rate decrease was attributed to an increase in flight duration (Fig. 1c), although the net weight of food

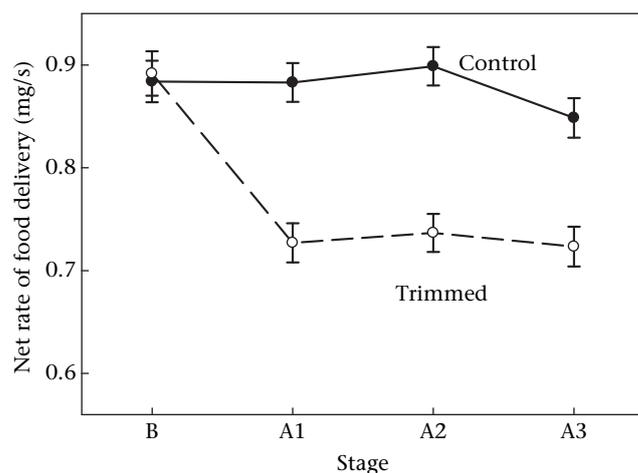


Figure 2. Average \pm SE net rate of food delivery before (stage B) and after (stage A1) wing trimming and sham control, and on two successive days (stages A2 and A3) ($N = 18$ bees from 9 matched pairs).

decreased as well (Fig. 1b). The fact that foragers weighing approximately 80 mg could still carry nectar loads of about 60 mg to the hive after losing 20% of their front wings indicates an extraordinary versatility of the bees' flight machinery. This flexibility most likely resulted from rapid changes occurring immediately after wing trimming because, contrary to our expectations, wing-trimmed bees did not show improvements in performance either over the first few trips (Fig. 3) or over days following wing trimming (Figs 1, 2). Nor did the wing-trimmed bees reduce their departure body weight to compensate for the increase in wing loading.

While we understand well many aspects of insect flight behaviour (Dudley 2000), we know little about how insects adjust to wing damage, even though it is an inevitable part of their life. Measurements in unloaded bumblebees indicated an increase in the wing beat frequency following wing trimming (Hedenstrom et al. 2001). The exact behavioural changes in loaded foragers, however, have not been examined. It is likely that, in addition to increased wing beat frequency, wing damage results in a variety of subtle behavioural changes in flight behaviour, which could be examined via high speed video recording (see Combes et al. 2010). Such changes probably involve motor learning as well. Future studies examining the cognitive and behavioural changes that occur following wing

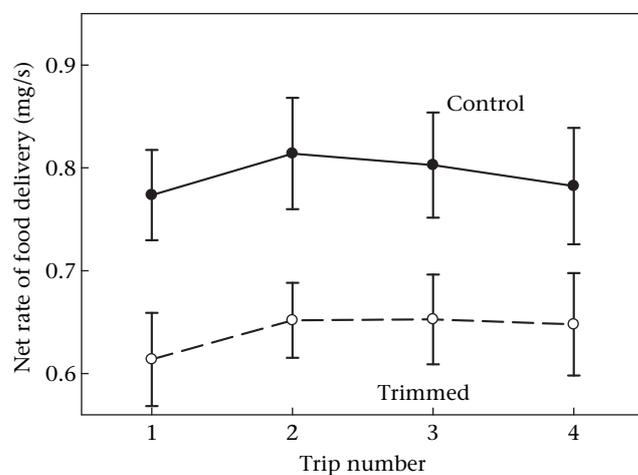


Figure 3. Average \pm SE net rate of food delivery in the four trips immediately following wing trimming and sham control ($N = 38$ bees from 19 matched pairs).

damage should focus on subjects' first flight after sustaining damage because we failed to detect changes indicating improved performance in later flights (Fig. 3). Further research may also examine the cost of maintaining the physiological plasticity required for adjusting to wing damage and whether bees experience more difficulties compensating for wing damage with age.

As expected (Cartar 1992), wing trimming reduced foragers' life span. At our field site, we documented a large value of age-independent mortality rate (13.4%, Dukas 2008a) and the expected life span of unmanipulated foragers was 4.5–6.3 days even when they visited a feeder located 400 m from the hive (Dukas 2008a, b, c). This suggests that the dominant cause of mortality at our site is predation rather than physiological deterioration associated with advanced age. Because predation very rarely occurs at the feeder, we know that predators capture bees as they fly between the feeder and hive. Hence, it is most likely that the decreased flight manoeuvrability associated with wing damage (Combes et al. 2010) decreased bees' abilities to escape predator attacks. Unfortunately, we do not know the predators' identities and cannot critically preclude the role of other factors such as adverse weather.

Our study includes the first quantification of the effect of wing damage on the net rate of food delivery, which relates the foraging performance of individual foragers to their colony fitness. While we could measure the flight duration from the feeder and the amount of food delivered, the use of a single feeder precluded us from examining natural flight behaviour between flowers, which is a relevant topic examined in a few studies (Higginson & Barnard 2004; Haas & Cartar 2008; Foster & Cartar, in press). This limitation can be resolved by using a modification of our set-up that includes a few artificial flowers (see Schmid-Hempel et al. 1985), which would allow one to quantify bees' flight behaviour as they carry progressively heavier loads between flowers.

Compared to other animal body parts that show nonrepairable damage, insect wings are more amenable to the empirical manipulation required for critically assessing how animals cope with non-repairable body damage. Most importantly, instead of observing individuals with naturally occurring damage, one can experimentally assign individuals to a given magnitude of damage and thus separate the specific effects of that damage from other factors that co-occur with natural ageing. For example, with natural wing damage, the most obvious concern is that the damage is tightly correlated with and perhaps even caused by the physiological deterioration of the flight machinery accompanying senescence (see Dudley 2000, page 196).

In summary, honeybees coped well with the loss of 20% of their frontal wings. Their overall net rate of food delivery remained rather high and only 20% below that of sham controls. The likely cost of the wing-damaged bees maintaining relatively high foraging performance was a corresponding increase in mortality rate, which appeared to be caused by predation.

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