



Trouble on takeoff: Crude oil on feathers reduces escape performance of shorebirds



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ABSTRACT

The ability to takeoff quickly and accelerate away from predators is crucial to bird survival. Crude oil can disrupt the fine structure and function of feathers, and here we tested for the first time how small amounts of oil on the trailing edges of the wings and tail of Western sandpipers (*Calidris mauri*) affected takeoff flight performance. In oiled birds, the distance travelled during the first 0.4 s after takeoff was reduced by 29%, and takeoff angle was decreased by 10° compared to unoiled birds. Three-axis accelerometry indicated that oiled sandpipers produced less mechanical power output per wingbeat during the initial phase of flight. Slower and lower takeoff would make oiled birds more likely to be targeted and captured by predators, reducing survival and facilitating the exposure of predators to oil. Whereas the direct mortality of heavily-oiled birds is often obvious and can be quantified, our results show that there are significant sub-lethal effects of small amounts crude oil on feathers, which must be considered in natural resource injury assessments for birds.

1. Introduction

Escaping predators is one of the main survival tasks for animals. Like most birds, migratory shorebirds have evolved behavioural tactics to minimize predation risk. Shorebirds can time migration in order to avoid the peak of migratory raptors on their journey (Ydenberg et al., 2004), and they travel in flocks using dilution or the confusion effect to reduce an individual's chance of being killed (Cresswell, 1994). To be effective, these behavioural tactics must be accompanied by the appropriate ability to fly and manoeuvre. In particular, when an attack occurs, individuals that are slow or become separated from the flock are most vulnerable. Takeoff performance is therefore one of the major aspects of predation avoidance for migratory shorebirds and other flocking birds.

Difficulties during takeoff can occur when individual birds moult flight feathers (Swaddle and Witter, 1997; Swaddle et al., 1999), or when wing loading (the weight of the bird relative to its wing area) is high (Burns and Ydenberg, 2002; Ortega-Jiménez et al., 2010). External factors such as natural feather abrasion, breakage, or sun damage may

also reduce feather quality and takeoff performance. Feathers can become contaminated with crude oil during oil spills, and whereas the inability of heavily-oiled birds to fly is often obvious, the potential for small amounts of oil to impair flight performance has not been studied.

During the 2010 Deepwater Horizon (DWH) oil spill in the Gulf of Mexico, about 3.2 million barrels of crude oil were discharged in the sea over an uninterrupted period of about three months (NOAA, 2015). The spill affected at least 25,000 km² of marine habitat and over 2100 km of coastal habitat (NOAA, 2015) in the Gulf of Mexico region. Both resident and transient birds, such as migratory shorebirds, were affected by the spill and their exposure to crude oil persisted long after the discharge from the compromised well was stopped (NOAA, 2015). Previous studies have typically only considered the acute effects of oil leading to rapid death, such as toxicity after ingestion and the reduced insulation of oiled feathers (Peakall et al., 1982; Fry and Lowenstine, 1985). During the DWH spill, tens of thousands of birds were estimated to have been directly killed, and several thousand live oiled birds were also observed (NOAA, 2015). The majority of these birds were assigned

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to “trace” or “light” oiled categories (less than 5% and 5–20% of body surface, respectively).

We quantified for the first time the effects of crude oil on takeoff ability of birds. We hypothesized that birds with lightly-oiled wing and tail feathers, as are commonly observed during oil spills, would have reduced takeoff performance (slower speed and lower takeoff angle). We studied the effects on wings and tail because these are the major surfaces involved in creating lift during flight (Thomas, 1997; Pennycuik, 2008), and we expect takeoff to be impacted when these surfaces are not fully functional, as in the case of oil contamination. We used high-speed video and three-axis accelerometers to quantify the effects of feather oiling on takeoff of western sandpipers. High-speed video is a standard method used to measure takeoff speed and angle (Lind et al., 2010). Accelerometers are used to measure parameters that are relevant to takeoff, such as overall dynamic body acceleration (ODBA), which has been shown to indicate mechanical power output in a variety of animal species, including birds (Wilson et al., 2006; Halsey et al., 2009; Elliott et al., 2013; Duriez et al., 2014). Measuring ODBA allowed us to deepen our understanding of the energy requirements of takeoff in birds with flight feathers contaminated by crude oil.

2. Materials and methods

2.1. Study birds

Western sandpipers (family Scolopacidae) winter in the Gulf of Mexico in large numbers (Morrison et al., 1993; Nebel et al., 2002), and were one of the species exposed to MC252 oil from the DWH spill (NOAA, 2015). They are representative of other birds of similar size and habitat requirements.

We captured western sandpipers near Roberts Bank and Boundary Bay in Delta, British Columbia, Canada (49°04'N; 122°58'W) in July 2012 and July 2013. Upon capture they were held for up to one week in animal facilities at Simon Fraser University (Burnaby, BC, Canada) before same-day shipment to Toronto, Ontario, Canada. They were then transported by vehicle to the Advanced Facility for Avian Research (AFAR) at the University of Western Ontario, London, Ontario, Canada and maintained in captivity until the experiments.

The birds were housed in specialized 2.4 m × 3.7 m shorebird rooms under 16L:8D (16 h of light, 8 h of darkness) light conditions at approximately 22 °C. They were fed an ad libitum diet of 80% Mazuri Waterfowl Starter (Purina, Agribands Purina Canada, Woodstock, ON, Canada) and 20% trout chow (Aquamax Fingerling Starter 300, Grey Summit, MO, USA) supplemented with ~50 mealworms/20 birds every other day. During winter 2013 the light cycle was switched to 12L:12D to simulate conditions on the winter range. In mid-April 2013 the light cycle was changed to 14L:10D to photostimulate the birds into a migratory condition. The test in June 2013 was performed under these photoperiodic conditions. The birds captured in July 2013 were tested in September 2013 and the tests were performed when they were experiencing 16L:8D. During the winter 2013–2014 they went through the same photoperiodic changes described above, and additional tests were performed while the birds were experiencing 14L:10D.

2.2. Study design and schedule

The study was performed in three sessions: the first in June 2013 using birds caught in July 2012 (N = 10 oiled), the second in September 2013 using birds caught in July 2013 (N = 7 oiled, N = 7 controls), and the third in November 2014 (N = 7 oiled, N = 6 controls). In June 2013 and September 2013, the birds were tested sequentially over four days: baseline flight without accelerometer (video only), baseline flight with accelerometer, oiled (or sham) flight without accelerometer, and oiled (or sham) flight with accelerometer.

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.ecoenv.2017.03.026>.

Due to an unrecoverable data storage drive failure, the September 2013 videos were lost before they could be analyzed. We analyzed the accelerometer data from September 2013, but we waited until November 2014 to repeat the video recordings to allow the birds to replace their feathers, and to measure them while they were in a similar migratory state. We repeated the time-matched control experiment (see below) with the same individual birds that were studied in September 2013, except that in this case birds were measured over two days with the baseline followed by the experimental flight.

We followed a four-day protocol: all birds flew baseline flights (BF) on day one (video only) and two (video and accelerometer), and then were oiled or sham-treated on day three for their experimental flights (EF, video only). On day four they flew an additional flight carrying accelerometers. Between day three and four the sandpipers were held without access to bathing pools so their feathers remained oiled until tested on day four. In June 2013 all birds were oiled after their baseline flights. In September 2013 and November 2014 we added a time-matched control group to exclude the possible effect of habituation to the experimental schedule. Accelerometers were only deployed in June 2013 and September 2013.

2.3. Application of crude oil to feathers

The oil applied to the birds from the oiled group was MC 252 oil collected during the 2010 DWH Gulf of Mexico oil spill and artificially weathered (TDI-Brooks International, College Station, TX) prior to receipt for use in the studies. Birds from the oiled group were oiled on 25% of the total surface of wings and tail. Oil covered the tip of the primary feathers and tail feathers (Fig. 1). This level of oiling represented approximately 20% of the total body surface (light oiling) as determined from study skins in advance of the study, however, in a standing bird, this represented less than 5% of the visible body surface.

2.4. Takeoff experimental procedure

We conducted the takeoff flights in a large, brightly lit animal room that was sub-divided by temporary walls and white curtains into a test arena (length 500 cm, width 310 cm, height 290 cm). At a release point near a corner of the arena, each bird was placed in an opaque box 20 cm above the ground surface and approximately 30 cm from a wall to the bird's left side. A high-speed video camera (Motion Pro X4 plus, Integrated Design Tools, Inc.) was positioned perpendicular to the release point and recorded the takeoffs at 200 frames per second (fps). The researcher waited until the bird positioned itself facing the long dimension of the arena (perpendicular to a side-view video camera and away from the researcher). At this point, the box was removed and an external stimulus (clicking sound produced by a dog-training clicker, one to three clicks) was given to induce takeoff. The observer behind the bird used angle markers on the ground to estimate the angle of deviation from the straight line perpendicular to the camera to correct

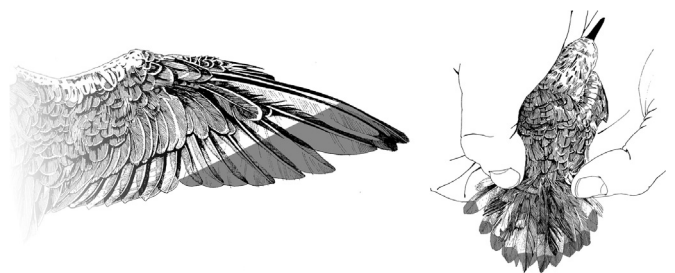


Fig. 1. Patterns of oiling for the experiments on Western sandpipers. Crude oil was applied to the trailing edge of the wing beginning 2.3 cm from the tip of the outermost primary feather to the tip of the 10th primary feather, and along a 0.7 cm margin of the tail. Sham treated birds were brushed in the same locations for the same duration with a dry paint brush. Illustration kindly provided by D.R. Smith.

for perspective. An example for such a video can be found in the supplementary materials. In addition to the video recordings, we deployed tri-axial acceleration loggers, which were custom-designed to minimize mass (Shafer et al., 2015). The accelerometers were fitted into a plastic bird-mount logger carrier and attached to the bird with a leg-loop harness, sized according to the bird's body weight following (Naef-Daenzer, 2007).

2.5. Accelerometers

We used tri-axial custom-made acceleration loggers. The logger board weighed 440 mg, and we used a plastic holder and harness that added 250 mg, for a total added mass of 690 mg, averaging roughly 2.3% of a bird's body mass. The acceleration logger employed an MSP430F2274 microcontroller from Texas Instruments (Dallas, TX, USA) and a BMA150 accelerometer from Bosch Sensortec (Reutlingen, Germany). The system was powered by a small rechargeable battery (Panasonic ML614). The microcontroller scheduled sensor readings and stored the data to local Flash memory, where it was read later. The BMA150 sensed three orthogonal axes of acceleration, had configurable sensitivity and sample rates, and used a 10 bit analog to digital converter. For this experiment, the BMA150 was configured to output 8 bit data, with a maximum range of $\pm 8g$ at 200 samples per second. This configuration yielded a minimum sensitivity of 62.5 millig (with g being the Earth's acceleration due to gravity). Data capture was initiated manually via a toggle switch before the start of each flight and continued until the onboard 30208 byte onboard memory was filled, which took 50.35 s. When the memory was filled, the bird was recaptured and the tag was read.

We obtained acceleration data from 7 out of 10 birds in June 2013 (3 accelerometers failed) and all 14 birds in September 2013. In total, we had acceleration data for 21 birds: 7 oiled birds in June 2013, and 7 controls and 7 oiled birds in September 2013. The data obtained from the accelerometers were accelerations in g (with g being the Earth's acceleration due to gravity) in the x (forward), y (sideways), and z (vertical) axes at 0.005-second intervals.

To assess the energy required for takeoff from accelerometer data,

we calculated overall dynamic body acceleration (ODBA, measured in g , with g being the Earth's acceleration due to gravity), a comprehensive metric that includes both wingbeat amplitude and frequency. ODBA was calculated using two different equations:

$$ODBA(L1norm) = |A_{dx} - A_{sx}| + |A_{dy} - A_{sy}| + |A_{dz} - A_{sz}| \quad (1)$$

$$ODBA(L2norm) = \sqrt{(A_{dx} - A_{sx})^2 + (A_{dy} - A_{sy})^2 + (A_{dz} - A_{sz})^2} \quad (2)$$

where dynamic acceleration in direction i , A_{di} , was the acceleration measured at that data point and static acceleration in direction i , A_{si} , was the average of acceleration over 0.5 s before and after the data point. To select whether to use the L1 or the L2 norm for calculating ODBA, we chose 5 representative flights and calculated the regression coefficient between the two norms. The correlation between the L1 and the L2 norm for ODBA was very high ($R^2 = 0.996$), therefore we used the L1 norm (Eq. (1)) for analyses.

We determined flight duration as the number of seconds that the bird was actively flying by visually inspecting the accelerometer traces. Flight start and end were defined by the beginning and end of a rhythmic change in the z -axis of acceleration. Even though duration per se was not important if considering takeoff (for which the most important phase is within the first 0.5 s of flight), assessing duration was important to be able to exclude from our analysis any measurement taken after the bird landed.

2.6. Data analysis

2.6.1. Video data (takeoff speed and angle)

The video evaluation included the estimation of distance flown and takeoff angle at intervals of 0.1 s (20 frames) after the feet of the bird left the ground. Most birds were off-frame by 0.5 s, and we therefore have data on distance and angle at 0.1, 0.2, 0.3, 0.4 and 0.5 s after takeoff. The position of the bird at the moment when the feet first left the ground and every 20 frames was determined using software Image J 1.47 (National Institutes of Health, <http://rsb.info.nih.gov/ij/>). Using the software, we could determine the distance travelled and angle relative to the starting position at every time point. Distance was

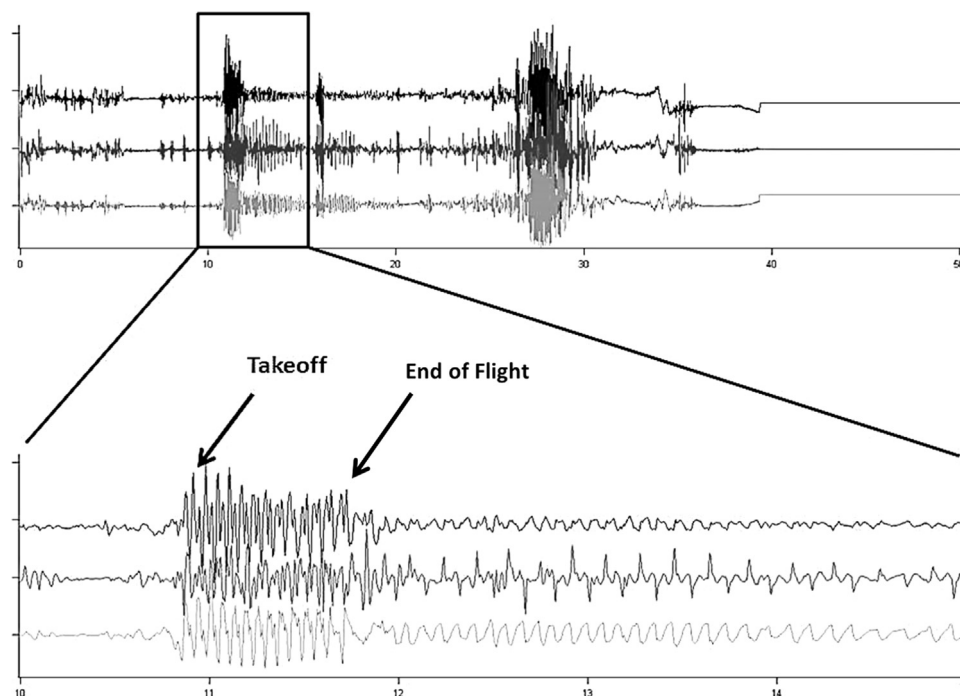


Fig. 2. Example of an accelerometer trace. The y-axis of the graph is arbitrary to ease viewing and the fluctuations in the lines represent wingbeats. The black upper line represents vertical acceleration (on the z -axis), the dark grey central line forward acceleration (on the x -axis), and the light grey lower line sideways acceleration (on the y -axis). The flight duration was determined to be during the period where oscillations in all three axes were large and rhythmic.

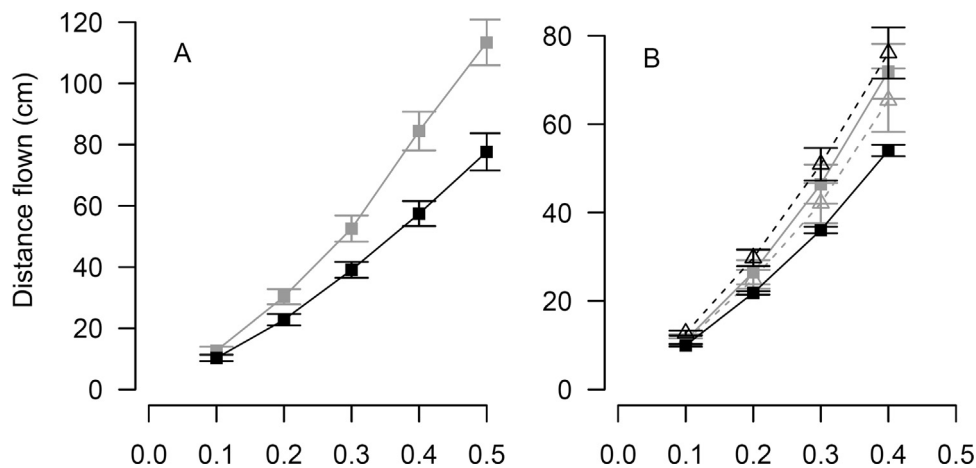


Fig. 3. Distance flown by Western sandpipers as a function of time after takeoff. (A) in the June 2013 experiment (N =10: ANCOVA intercept $F_{1,63} = 395.543$, $p < 0.001$; flight type (baseline or oiled) $F_{1,63} = 65.158$, $p < 0.001$; time $F_{1,63} = 1015.894$, $p < 0.001$; flight type*time $F_{1,63} = 30.393$, $p < 0.001$); (B) in the November 2014 experiment (N =14: intercept $F_{1,37} = 6.747$, $p = 0.013$; treatment (oiled or un-oiled) $F_{1,11} = 12.770$, $p = 0.004$; time $F_{1,37} = 25.922$, $p < 0.001$; treatment*time $F_{1,37} = 33.934$, $p < 0.001$). Oiled treatment (solid lines and squares): grey = baseline flight, black = oiled flight. Control treatment (dashed lines and triangles): grey = baseline flight, black = experimental flight. Error bars represent standard errors.

corrected for perspective if the bird was not flying perpendicular to the camera using the formula:

$$\text{Distance(corrected)} = \text{Distance(measured)} / \cos(\text{angle of deviation}) \quad (3)$$

where the angle of deviation (estimated by the observer behind the bird) was in radians.

We tested for effects of oiling by analyzing how distance (or angle) changed with time in oiled and un-oiled birds. For the June 2013 data we created a linear mixed model with distance (or angle) as the response variable (y), flight type (baseline, non-oiled flight ‘BF’ or experimental, oiled flight ‘EF’), time (0.1–0.5 s), the flight type*time interaction, and body mass as fixed factors, and individual as a random factor. Since the values at every time point are correlated with the previous time point, we added an autocorrelation structure (compound symmetry) to the model. In the model for distance, angle was also included as a fixed factor. The models were simplified by removing non-significant terms and the AICs of each model were compared in order to choose the best final model. One bird was excluded from the analysis since it was a clear outlier in both its BF and EF flights (it flew off at a

very steep angle).

To avoid the complicated interpretation of three-way interaction terms (treatment*time*flight type), but maintain a similar statistical approach for analysis of the November 2014 data, we modeled the difference in distance (or angle) between BF and EF for every individual using a linear mixed model. This allowed removal of flight type from the predictors, and a more straightforward interpretation of the results. The difference in body weight between BF and EF was added as a covariate in the models, and the difference in angle was added as a covariate in the model for difference in distance. As in the previous analysis, non-significant terms were removed from the model, and only the output of the final models is shown. We only considered the first 0.4 s of flight (rather than the first 0.5 s) because most of the birds were out of frame after that time and the sample sizes at time = 0.5 s were considerably smaller and highly unbalanced.

2.6.2. Accelerometer data (ODBA)

In a first step of the analysis we integrated ODBA over each wingbeat. In addition, as ODBA varies with time since takeoff, but is

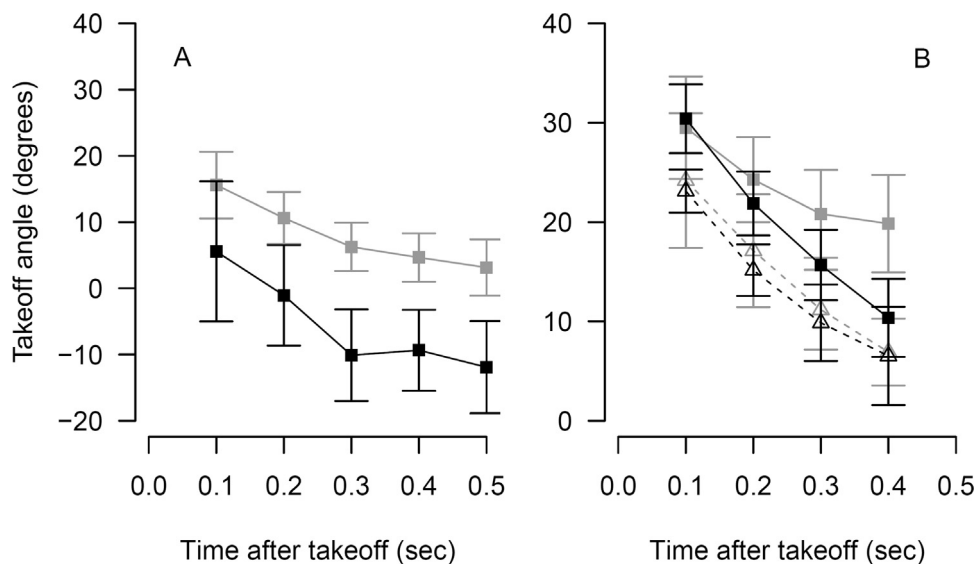


Fig. 4. Flight angle of Western sandpipers at different time points after takeoff. (A) in the June 2013 experiment (N = 10: ANCOVA intercept $F_{1,62} < 0.001$, $p = 0.998$; flight type $F_{1,62} = 27.501$, $p < 0.001$; time $F_{1,62} = 16.565$, $p < 0.001$; body mass $F_{1,62} = 0.434$, $p = 0.512$; flight type*time $F_{1,62} = 0.685$, $p = 0.411$); (B) in the November 2014 experiment (N = 14: intercept $F_{1,37} = 0.581$, $p = 0.451$; treatment $F_{1,11} = 0.159$, $p = 0.698$; time $F_{1,37} = 11.001$, $p = 0.002$; treatment*time $F_{1,37} = 12.577$, $p = 0.001$). Oiled treatment (solid lines and squares): grey = baseline flight, black = oiled flight. Control treatment (dashed lines and triangles): grey = baseline flight, black = experimental flight. Error bars represent standard errors.

only a useful variable when averaged over several wingbeats, we averaged ODBA over 0.25-second intervals, representing roughly four wingbeats. We considered the takeoff to begin once the wingbeat amplitude started to increase from baseline by visually inspecting the accelerometer output. See Fig. 2 as an example. Wingbeats were separated by subsequent minima in the z-axis of acceleration.

For the sake of investigating patterns, in a first step we analyzed each treatment group and season separately (i.e. the June 2013 oiled birds, the September 2013 controls, and the September 2013 oiled birds). We ran linear mixed models with ODBA as the response variable (y), flight type (BF or EF) and body mass as fixed factors, and individual as a random factor. We ran a model for each of the first 20 wingbeats, respectively the first eight 0.25 s-intervals (i.e. each interval for the first 2 s of flight). The models yielded no significant differences between flights, but tendencies were noted. To investigate these patterns more closely we modeled the difference in ODBA between BF and EF at each wingbeat/interval. We included treatment, wingbeat/interval, the difference in body mass between BF and EF and the treatment*wingbeat/interval interaction as fixed factors, and individual as a random factor. As described above, we modeled differences instead of absolute values in order to avoid the difficult interpretation of the three-way interaction of interest (treatment*flight*wingbeat/interval) by removing flight as a fixed factor. We merged wingbeats/intervals with similar differences in ODBA using contrasts (Crawley, 2007) to simplify interpretation. For every simplification step we tested for changes in the model deviance and stopped simplification when the change was significant (Crawley, 2007).

All statistical analyses were performed using the software R 3.0.2 (R Core Team, 2012).

3. Results

Video recordings of takeoff flights were made with two different groups of sandpipers in June 2013 (N = 10) and in November 2014 (N = 14). See Section 2 for details of the experimental schedule, however, in brief, in June 2013 we measured all birds with oiled feathers following a baseline flight test, whereas in November 2014 we included time-matched controls which received no oil on their second flight. Birds that were oiled flew a significantly shorter distance (y) per unit time than in their baseline flight (Fig. 3). Similarly, oiled birds flew at a lower angle relative to their baseline flight (Fig. 4). The oiled group had higher takeoff angles than the control group already in their baseline flight (Fig. 4B). This was the result of randomly selecting birds with generally higher takeoff angles. However, while controls repeated their performance in their second flight, the oiled group significantly decreased their takeoff angle after oiling. In the November 2014 experiment the time-matched controls maintained the same distance and angle in the sham-oiled treatment flight as in their baseline flight (Figs. 3b and 4b). Within 0.4 s after takeoff, oiled birds covered 29% less distance than on the baseline flight (data of both experiments combined: average distance covered on baseline flight = 73.7 cm; oiled flight = 52.1 cm), and they flew at about a 10° lower angle than when unoiled.

The reduction of takeoff speed in oiled birds tended to be coupled with a decrease in ODBA averaged over groups of wingbeats, beginning from the third wingbeat after takeoff (wingbeats were grouped as follows: 1–2: “early”, 3–20: “late”, Fig. 5). When averaging ODBA over time intervals rather than wingbeats, the opposite pattern was observed: ODBA tended to be less during the initial part of the takeoff and greater later on (intervals were grouped as follows: 0.00–0.25 s after takeoff: “initial”, 0.25–0.75 s: “median”, 0.75–2.0 s: “late”, Fig. 6).

4. Discussion

Western sandpipers with crude oil on the trailing edges of their wings and tail took off more slowly and flew at a lower angle than

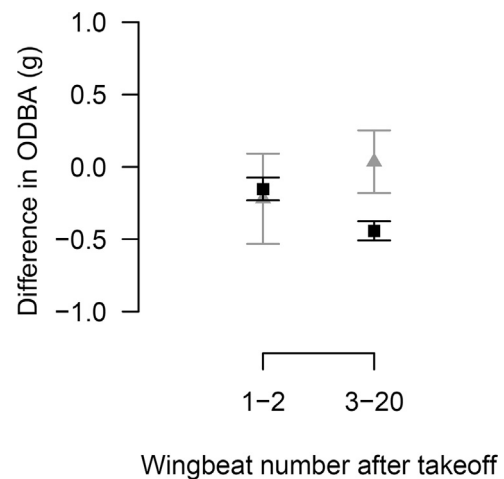


Fig. 5. Difference in ODBA between baseline and experimental takeoff flights of Western sandpipers for the first 20 wingbeats. Groups of wingbeats were merged during analysis and grouped into “early” (wingbeats 1–2) and “late” (wingbeats 3–20). Grey triangles: control group; black squares: oiled group. Differences were not significant (intercept $F_{1,356} = 6.952$, $p = 0.009$; treatment $F_{1,18} = 0.660$, $p = 0.427$; wingbeat $F_{1,356} = 5.132$, $p = 0.024$; treatment*wingbeat $F_{1,356} = 3.631$, $p = 0.058$).

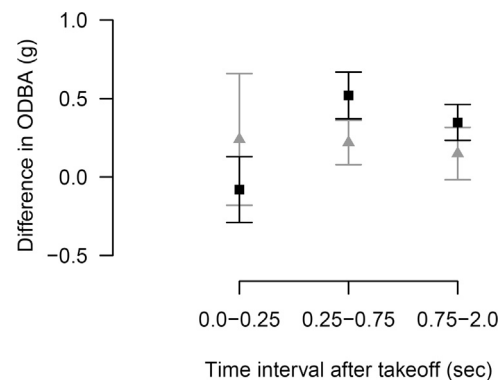


Fig. 6. Difference in ODBA between baseline and experimental takeoff flights of Western sandpipers for the first 2 s of flight. Time after takeoff was divided in intervals of 0.25 s. Groups of intervals were merged during analysis and grouped as “initial” (0.0–0.25 s after takeoff), “median” (0.25–0.75 s), and “late” (0.75–2.0 s). Grey triangles: control group; black squares: oiled group. Differences were not significant (intercept $F_{1,65} = 8.116$, $p = 0.006$; Treatment $F_{1,18} = 0.061$, $p = 0.808$; Interval $F_{2,65} = 2.652$, $p = 0.078$; treatment*interval $F_{2,65} = 1.227$, $p = 0.300$).

control birds. Feather damage is likely to affect flight performance by decreasing lift and thrust, increasing drag, imbalance, and difficulties to take off (Beaufrère, 2009). The effects of feather damage caused by external oil contamination on flight, however, had not previously been examined. Though we have no indications about what properties of the feathers were affected by the oiling, we were able to demonstrate a strong effect on takeoff performance.

Migrating sandpipers feed in large flocks, and their stopover site selection is determined by both food availability and predation risk (Ydenberg et al., 2002). Above a certain body mass (about 26 g), western sandpipers had lower take-off ability and selected safer but less profitable stopover sites (Ydenberg et al., 2002). Refueling at a stopover site in sandpipers is optimized to reach a body mass high enough to resume migration within a short time (Alerstam and Lindström, 1990; Hedenström and Alerstam, 1997). Switching to less rewarding stopover sites, therefore, can cause delays to the overall migration (Lindström, 2003). A study of western and least sandpipers (*Calidris minutilla*) documented a 20% reduction in takeoff speed over the range of natural wing loadings studied (Burns and Ydenberg, 2002). Our observation of a 29% reduction in distance covered in oiled birds (which is equivalent to the relative reduction in speed during the given time range of 0.4 s) is

even larger than the natural variation in speed caused by variation in body mass. Thus, lightly oiled birds may limit their refueling activity to safer sites, reducing fuel deposition rate and delaying migration.

Oiled western sandpipers tended to produce less mechanical power per wingbeat than controls, as indicated by their lower ODBA values over the first two wingbeats. On the other hand, ODBA averaged over time intervals was slightly greater for oiled birds during the initial part of the flight. These differences were not statistically significant due to the large variation in the data. However, this suggests that oiled sandpipers may compensate for reduced power output by increasing their effort via greater wingbeat frequency. Despite the apparent added effort, oiled birds were unable to achieve the same performance (as indicated by flight distance) as controls. Additional studies are required to elucidate the mechanisms by which crude oil changes feather properties and the relationship between oiling and the power requirement/output during takeoff in oiled birds.

The significance of a 29% speed reduction at takeoff is reflected in several different potential impacts due to predation by raptors (the main predators of shorebirds on migration). Raptor predation success is increased if the prey is isolated from the flock (Buchanan et al., 1988), remains at the periphery of the flock (Jennings and Evans, 1980; Inglis and Lazarus, 1981), takes off slower (Whitfield, 1985), or needs a longer time to reach cover (Bednekoff, 1996). It takes 0.25–0.7 s for an entire flock of shorebirds to initiate and complete a takeoff (Hilton et al., 1999), indicating that our study addressed the biologically relevant time frame. This also means that after about one second, the delay due to oiling of feathers would be similar to that associated with being the last bird to take flight, assuming an average flock takeoff time of 0.5 s. Oiled birds might thus stand out and become preferred targets for predators. As a result, during an oil spill, the reduced escape performance of oiled birds could disproportionately impact higher trophic levels if raptors and other predators selectively capture and consume them.

Some different scenarios could arise as an effect of decreased escape performance of shorebirds in a flock. One possibility is that the overall decrease in the population would remain constant, in the case where the number of raptor attacks remains the same, but their efforts would be directed preferably towards oiled birds (a version of the “doomed surplus” hypothesis, Errington, 1945). This would not impact the overall sandpiper population, but would possibly cause toxicological effects on the predators (Zuberogaitia et al., 2006). Alternatively, the presence of escape-impaired individuals in the flock might attract additional predators that usually prey on shorebirds only in rare occasions, such as harriers or caracaras (Page and Whitacre, 1975; Nebel and Ydenberg, 2005). Lastly, oiled sandpipers might choose safer, less profitable stopover sites where predation is reduced (Ydenberg et al., 2002). Due to the lower profitability of these sites, and to the time take to remove the oil, this might result in delays of migration and late arrival at the breeding sites, with consequences on reproductive success (Sandercock et al., 1999).

A great number of oiled birds observed in the aftermath of spills are assigned to “trace” and “light” oiled categories, but damages to them are often overlooked or poorly quantified (Timoney and Ronconi, 2010). Our findings show that even small amounts of oil can negatively impact escape flight performance of birds. The negative effects of oil on sprint locomotion in birds contribute to putting them at greater risk of mortality, and should be considered in resource injury and environmental impact assessments during oil spills.

Ethical standards

This research is in compliance with regulations governing animal research. Bird capture, housing, and experiments were performed under the guidelines of the University of Western Ontario Animal Use Subcommittee (protocol 2012-027) and according to permit CA-0256 from the Canadian Wildlife Service.

Author contributions

I.M. and C.G.G. conceived the idea and designed the study, K.D. and C.A.P. participated in designing the study, I.M., L.V.K., A.M., C.G.G. and K.H.E. performed the experiments, I.M. and C.G.G. wrote the manuscript, I.M. and C.G.G. developed the methods, I.M. and K.H.E. analyzed the data, R.M. provided the accelerometers, advised on data analysis, and wrote sections of the manuscript. All authors have read and approved the final version of the manuscript.

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