

**Foraging behavior and flight dynamics of rhinoceros
auklets (*Cerorhinca monocerata*) experimentally
dosed with diluted bitumen**

**by
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Abstract

Seabirds have long been used as “bioindicator” species in eco-toxicological monitoring, but most studies related to oil pollution have involved conventional crude oils. The majority of current Canada’s oil production involves highly viscous oil sands bitumen, which must be diluted in order to enable transport through pipeline (i.e. “dilbit”) but virtually nothing is known about dilbit toxicity in birds. I used GPS-accelerometers in free-living Rhinoceros Auklets (*Cerorhinca monocerata*) combined with internal and external dilbit dosing to investigate effects on reproduction, foraging and diving behaviour. There was no effect of treatment on retrieval rates, mass change of adults during deployment, or chick mass gain. Chicks raised by externally-dosed birds had reduced wing growth at day 25 compared to internally-dosed or control birds. There was no difference in trip length in relation to treatment. Within their daily time-activity budget, internal-dosed birds spent less time diving and more time swimming compared to external-dosed birds, with control birds being intermediate. We used accelerometers to calculate wing-beat frequency (WBF), wing-beat amplitude (WBA), overall dynamic body acceleration (ODBA) and pitch; for each of these metrics, there was substantial overlap in values between treatments. I discuss why our dilbit treatment had few significant effects and suggest future directions for research on dilbit.

Keywords: oil pollution; diluted bitumen; accelerometry; *Cerorhinca monocerata*

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Table of Contents

Declaration of Committee	ii
Ethics Statement	iii
Abstract	iv
Acknowledgements	v
Table of Contents	vi
List of Tables	vii
List of Figures	viii
Chapter 1. Introduction: seabirds as sentinels of marine ecosystem health.....	1
1.1. Seabirds and Oil Pollution	4
Chapter 2. Effects of diluted bitumen exposure on reproductive success, flight and diving behaviour of free-living Rhinoceros Auklets (<i>Cerorhinca monocerata</i>).....	7
2.1. Introduction.....	7
2.2. Materials and methods	10
2.2.1. Study species.....	10
2.2.2. Burrow Monitoring and Treatment Application.....	10
2.2.3. GPS and accelerometer deployment.....	11
2.2.4. Analysis of GPS/accelerometer data	12
2.2.5. Statistical analysis.....	15
2.3. Results	16
2.3.1. Deployment success and mass change during deployment	16
2.3.2. Effects of treatment on chick growth.....	17
2.3.3. Effects of dilbit treatment on foraging trips and behaviour	19
2.3.4. Effects of dilbit treatment on diving behaviour	20
2.3.5. Effects of dilbit treatment on flying behaviour	26
2.4. Discussion	29
2.4.1. Deployment success and tag effects	29
2.4.2. Treatment effects on chick growth.....	31
2.4.3. Treatment effects on foraging trip duration and overall activity	31
2.4.4. Treatment effects on diving behaviour.....	32
2.4.5. Treatment effects on flight dynamics	33
2.4.6. Effectiveness of treatment in light of few significant results	34
2.5. Conclusion and implications for dilbit transport in the Salish Sea.....	36
References	39
Appendix A. Chick survival and growth rates by year and treatment for all deployments	52

List of Tables

Table 1. Mass change during deployment (g). Values are means \pm standard deviation. Sample size is given in parentheses.	16
Table 2. Chick mass (g) and wing length (mm) at 5 and 25 days old in relation to treatment. Values are means \pm standard deviation; sample sizes are in parentheses	18
Table 3. Length of foraging trips (hours) and percentage of time in each activity by treatment. Values are means \pm standard deviation. Sample size is given in parentheses	19
Table 4. Variation in maximum dive depth (m) and dive duration (sec) in relation to treatment for daytime and nighttime dives. Values are means \pm standard deviations; number of dives is in parentheses.	21
Table 5. Variation in wing-beat frequency (Hz), wing-beat amplitude (G) and ground speed (km/hr) during commuting flights in relation to dilbit treatments. Values are means \pm standard deviations. Number of seconds spent is in parentheses.	27

List of Figures

- Figure 1. Relationship between initial adult mass (g) and the change in mass during the deployment period..... 17
- Figure 2. Boxplot with interquartile ranges (IQR) showing variation between treatments in percentage of the foraging trip spent a) diving and b) swimming. Solid horizontal lines are the medians and error bars are the 95% confidence interval. Dots are outliers that lie 1.5 x IQR from the median.....20
- Figure 3. Boxplot with interquartile ranges (IQR) showing variation between treatments and time of day for a) maximum dive depth (m) and b) dive time (sec). Points are outliers that lie 1.5 x IQR from the median.....22
- Figure 4. Boxplot with interquartile ranges showing individual variation between (top) mean dive depth and (bottom) mean dive duration for all individuals (n = 22), arranged by dilbit treatment. The horizontal line indicates the overall mean.....23
- Figure 5. Relationship between dive depth (m) and dive duration (s). Red lines indicate slope b; in a) slope = 2.04 for all dives, in b) the slope is 4.04 for dives < 10 m depth and 1.1 for dives > 10 m depth. Only daytime dives are included.24
- Figure 6. Descent rate (m/s) during the descent phase of diving by current depth. Dives are binned by 5m intervals by the maximum depth achieved during the dive. Error bars are one standard deviation.....25
- Figure 7. ODBA during the descent phase of diving by current depth. Dives are binned by 5m intervals by maximum depth achieved during the dive. Error bars are one standard deviation.....26
- Figure 8. Boxplot with interquartile ranges (IQR) showing individual variation between all individuals (n = 22), for (left) Mean wing-beat frequency (Hz) and (right) amplitude (G) during commuting flights. Solid points represent outliers that are 1.5 x IQR away from the median.27
- Figure 9. Mean wing-beat frequency (Hz) by flight time (sec) for the first minute of flight, including the takeoff period. Error bars represent one standard deviation.28
- Figure 10. Foraging tracks for Rhinoceros Auklets for both years of deployments (n = 22). Colours represent treatments, star denotes the colony on Middleton Island. Birds mainly foraged in the nearshore waters of Montague Island, although some birds foraged in pelagic waters north of the colony.....29

Chapter 1. Introduction: seabirds as sentinels of marine ecosystem health

Ocean pollution is a pervasive threat to the health of marine and coastal ecosystems caused by influxes of anthropogenic contaminants into the environment. Increasing levels of human coastal development, industry, and marine transport further threaten the health of these global ecosystems (Herbert-Read *et al.* 2022; Kvamsdal *et al.* 2023). There are many logistical difficulties in assessing levels of contamination in marine environments as they are often inaccessible and the pollution is often unpredictably and patchily distributed. The use of sentinel species, organisms which experience marine contamination in a biologically or ecologically relevant way, can mitigate some of these difficulties (Bossart 2011; Fossi & Panti 2017; Hazen *et al.* 2019). Understanding the specific effects of pollutants is critical to the use of these sentinel species as biomonitors and can inform risk assessment regarding potential pollutants.

Many researchers advocate the use of seabirds as sentinels of marine health. (Camphuysen 1997; Furness 1997a; Burger & Gochfeld 2004; Mallory *et al.* 2010; Elliott & Elliott 2013a). Seabirds have a long history of use as bioindicators of marine pollutants such as heavy metals (e.g. mercury), oil and other petroleum products, xenobiotics such as flame retardants, polychlorinated biphenyls (PCBs), dichlorodiphenyltrichloroethane (DDT) and, more recently, plastics (Camphuysen 1997; Furness 1997; Burger & Gochfeld 2004; Mallory *et al.* 2010; Elliott & Elliott 2013). Seabirds possess multiple traits that make them practical options for ecotoxicology monitoring. They are top trophic predators with large foraging ranges, making them useful indicators of bioavailability and bioaccumulation of contaminants, but unlike many other top marine predators they can be routinely accessed by researchers in a central location at their terrestrial nesting colonies (Piatt *et al.* 2007). Additionally, their colonial-nesting nature makes it more practical to obtain higher sample sizes of eggs or tissues for contaminant analysis (Furness 1997b; Elliott & Elliott 2013b). There are multiple non-lethal sampling methods available when using seabirds (e.g. feathers, eggs, blood, biopsies) that, coupled with geographical information from biologging devices (e.g. radio-telemetry, GPS, accelerometers), can provide different spatiotemporal information on incorporated contaminants and chemical tissue residues. Differences in concentrations of contaminants between species with different life histories (such as surface vs. epipelagic

vs. benthic foragers or coastal vs. pelagic foragers) can also help illuminate the specific origin and distribution of contamination in the marine environment (Elliott & Elliott 2013; Bianchini et al. 2022).

In relation to heavy metal pollution, seabirds have been used as monitors of mercury in the marine environment for over two decades (Furness 1997b). Mercury from anthropogenic sources can be transported long distances in the atmosphere as elemental mercury (Hg^0), and eventually will settle and become deposited into aquatic systems. Sulfate-reducing bacteria can transform Hg^0 into the highly toxic methylmercury (MeHg), which is lipid-soluble, bioaccumulative and biomagnifying (Clarkson & Magos 2006). Seabirds mainly incorporate methylmercury from their diet, and as top predators they are often exposed to significant concentrations making them good candidates for monitoring (Monteiro & Furness 1995). In birds, major pathways for mercury excretion include feather synthesis and egg production (Lewis & Furness 1993; Monteiro & Furness 2001; Heinz & Hoffman 2004; Agusa *et al.* 2005). Tissue collection allows researchers to sample across a longer time-scale from a single bird, as the incorporation of mercury into various tissues varies annually; i.e. eggs provide information on mercury consumed during the pre-laying or laying period, feathers provide information on when they were grown during moult (which varies by feather type species), typically during the non-breeding phase, and nestling feathers and blood both provide immediate (breeding) measures of contamination. Feather samples for mercury analysis can be obtained from older, archived museum specimens, allowing for even longer time-series that can stretch back over a century (Thompson *et al.* 1998; Vo *et al.* 2011). Synthesizing mercury concentrations and stable isotope signatures, which provide information on a bird's trophic feeding level, provides a more complete picture of mercury's cycling and exposure pathways in marine food chains. (Thompson *et al.* 1998; Brasso & Polito 2013; Fort *et al.* 2014; Elliott & Elliott 2016). Due to mercury's spatial patchiness and bioaccumulative nature in the marine environment, it is important to disentangle effects of geographic variation and changes in food-chain level contamination. For example, Thick-Billed Murres (*Uria lomvia*) from Svalbard and Baffin Bay differed in their concentrations of mercury despite foraging at the same trophic level, suggesting that there was significant regional or geographical variation in mercury concentrations at specific foraging locations (Brasso & Polito 2013). In Little Auks (*Alle alle*), however, long-term studies of Hg concentrations and their zooplankton prey combined with stable-

isotopic analyses determined that increased Hg exposure was related to food-chain contamination rather than shifts in feeding behaviour (Fort *et al.* 2016). Movement data from Little Auks during the non-breeding season has also allowed the identification of specific regions of mercury contamination further away from the colony (Fort *et al.* 2014; Renedo *et al.* 2020).

Seabirds have also been used to monitor concentrations of persistent organic pollutants (POPs), such as organochlorine pesticides, polychlorinated biphenyls, and polybrominated diphenyl ether flame retardants (Lavoie *et al.* 2010; Yamashita *et al.* 2018; Bianchini *et al.* 2022). POPs are lipid-soluble and bioaccumulative and can therefore have substantial longevity in the environment as “legacy” contaminants. Eggs are typically used as a relatively non-destructive method of sampling POPs (Elliott *et al.* 1989; Braune 2007; Miller *et al.* 2014; Miller, Elliott, Elliott, Guigueno, *et al.* 2015; Braune *et al.* 2019), as pollutant concentrations are reflective of contaminant burdens within the female prior to laying and are transferred to the egg during egg formation (Bargar *et al.* 2001; Drouillard & Norstrom 2001; Bourgeon *et al.* 2013). For example, long-term monitoring of seabird eggs in the Canadian Arctic has been used as a reliable proxy for annual variation in levels of organic contaminants (Braune *et al.* 2019; Bianchini *et al.* 2022). Most seabirds that breed in the Arctic, especially those used for eco-toxicology monitoring, gather their resources for egg production in the local environment (Mallory & Braune 2012). However in other systems, such as egg monitoring on the Pacific coast, the contaminant load in eggs reflects its integration into the birds’ tissues on the wintering grounds. In conjunction with telemetry data, this can provide information on the spatial origin of contamination; for example, the contaminant burden of Rhinoceros Auklets tagged with geolocators best predicted by their wintering latitude rather than diet, suggesting variable contamination concentrations along the Pacific North American coast (Elliott *et al.* 2021). More recently, preen oil has been used to measure POPs, although it has key differences from eggs: it is measurable in both sexes, represents a more immediate level of contamination, and can be sampled multiple times in one individual within a season (Yamashita *et al.* 2018). In Japan, preen oil along with tracking data of has allowed for a finer-scale spatial resolution of contaminants; birds that foraged in the Seto Inland Sea had higher levels of PCBs than those that foraged in the Pacific Ocean off northern Japan (Ito *et al.* 2013; Yamashita *et al.* 2021).

More recently, seabirds have proven to be key biomonitors in the emergent field of plastic pollution (van Franeker et al. 2011; Provencher et al. 2015; Biamis et al. 2021; Sühling et al. 2022). Plastics, both from industrial and user sources, have been identified as one of the most pressing marine pollution issues globally. One of the first observations that highlighted the threat that plastics cause to marine fauna was its ingestion by seabirds and subsequent feeding of plastics to chicks; plastics were implicated in mortality of albatross chicks (Wood 1997) and also found in the gut contents of many stranded birds (van Franeker *et al.* 2011). Entanglement of birds in plastic debris was also identified as an early issue either at sea, especially from discarded fishing gear (Phillips *et al.* 2010; Ryan 2018), and due to the use of plastics by birds as nesting material which can trap and kill nestlings (Votier *et al.* 2011). Since then, concerns over different types of plastic pollution have evolved rapidly, and toxic and physiological effects associated with the ingestion of microplastics (plastic particles with a size of < 5 mm) have become a new focus of study. Research on seabirds has contributed to knowledge on a) how long (micro)plastics remain afloat on the surface (van Franeker *et al.* 2011), b) the amount and spatial distribution of plastics (Amélineau *et al.* 2016), c) plastic-mediated pathways for ingestion of other toxic chemicals that have adhered to the plastic's surface (Tanaka *et al.* 2019; Yamashita *et al.* 2021), and d) plastics-related diseases such as the newly named plastic-induced disease "plasticosis" caused by scarring of the proventriculus by ingested plastics (Charlton-Howard *et al.* 2023). Seabirds are also the focal taxon for the first established plastic monitoring program: incidences of plastics in the guts of Northern Fulmars (*Fulmarus glacialis*) in the North Sea have been tracked since 2002 (van Franeker *et al.* 2011; Provencher *et al.* 2015). Fulmars in particular are considered ideal candidates for monitoring due to their high abundance and wide distribution as well as their proclivity to ingest plastic and have it remain within their gut contents until death (van Franeker & Meijboom 2002).

1.1. Seabirds and Oil Pollution

In addition to the above-mentioned anthropogenic pollutants, seabirds have also been used as monitors of pollution associated with oil and gas production and transport. Petroleum, such as crude oils, include a variety of physical and chemical hydrocarbon mixtures often used as fuel. Human sources of petroleum into the marine environment include accidental spills and discharges often related to the production and

transportation of oil and gas products (Chilvers et al. 2021). Every oil spill is unique: the volume and composition of the released petroleum product, marine conditions, and location can all impact the fate of the oil and the ensuing ecological damage (Kingston 2002; Barron et al. 2020). Large catastrophic spills such as those from oil-tanker vessel accidents, pipeline spills or well blowouts, are well documented to have dramatic acute effects such as mass mortality and cause long-term damage that may take years to recover (Piatt & Lensink 1989; Piatt *et al.* 1990; Irons *et al.* 2000; Votier *et al.* 2005; Barron *et al.* 2020). For example, the 1989 grounding of the tanker vessel Exxon-Valdez in Prince William Sound, Alaska, caused the immediate mortality of an estimated 250,000 seabirds, and some species demonstrated oil toxicity and suppressed populations as much as two decades later (Piatt et al. 1990; Esler et al. 2000). Although they are less dramatic and consequently less publicized, smaller spills and chronic contamination (including both accidental and intentional vessel discharges along shipping lanes and emissions from offshore oil and gas platforms) are also damaging and can cause significant mortality (Camphuysen 1998; García-Borboroglu et al. 2006; Dong et al. 2022).

Seabirds are particularly vulnerable to oil pollution via contamination during oil spills, as oil leaked into the environment tends to accumulate in slicks upon the water surface where seabirds rest and forage (Leighton 1993; King *et al.* 2021). Physical contact with oil can compromise the structural integrity of a bird's plumage by causing feather barbs and barbules to clump (O'Hara & Morandin 2010; Morandin & O'Hara 2014; Whitmer *et al.* 2018; Matcott *et al.* 2019). Oil-damaged plumage loses its ability to repel water, which can impact a bird's thermoregulation and metabolic rate even at moderate levels of oiling (Hartung 1967; Erasmus *et al.* 1981; Butler *et al.* 1986; Culik *et al.* 1991). Oiled plumage can also have sublethal effects on a bird's flight or diving performance through increased drag (Maggini, Kennedy, Elliott, *et al.* 2017) or reduced buoyancy (Clark & Gregory 1971), which can cause a bird to expend more energy during locomotion (Maggini, Kennedy, Macmillan, *et al.* 2017), or take suboptimal flight paths (Perez *et al.* 2017a). Oiled birds may therefore be less effective foragers and rapidly exhaust their fat reserves, as evidenced by the emaciated state of oiled seabird carcasses (Oka & Okuyama 2000; Simpson & Fisher 2017). Oil may be ingested either directly from the environment, through consumption of contaminated prey, or indirectly by the preening of fouled plumage. Ingested oil can cause a diverse range of toxic

effects depending on the specific chemical composition of the crude or the mechanism of exposure (Hartung 1967; Leighton 1993). Toxic effects from ingestion of polycyclic aromatic hydrocarbons (PAHs), a class of compounds present in crude oil, can cause various pathological effects in birds, such as damage to internal organs, endocrine disruption (Peakall *et al.* 1981; Troisi *et al.* 2016), and hemolytic anemia (Leighton *et al.* 1983; Troisi *et al.* 2007; Fallon *et al.* 2020). Oil spills can have acute or long-term effects on a species' survival rates and breeding success with potential long-term implications for its population (Eppley & Rubega 1990; Esler *et al.* 2000; Votier *et al.* 2005; Pérez *et al.* 2008).

While there have been a large numbers of studies on effects on conventional oil and gas products (reviewed in King *et al.* 2023) there is a lack of available research on the toxicity of non-conventional crude oils. For example, currently the majority of Canada's oil production involves highly viscous oil sands bitumen, which must be diluted in order to enable transport through pipeline (i.e. diluted bitumen or « dilbit »). Virtually nothing is known about effects of exposure to dilbit in birds, with knowledge restricted to laboratory studies on captive zebra finches (Ruberg *et al.* 2022) and seabird eggshells (King *et al.* 2022), both of which demonstrated acute and sublethal toxic effects. However, laboratory studies do not necessarily reflect the conditions faced by wild birds, which also must contend with the challenges of survival (King *et al.* 2021). Therefore, in Chapter 2 I describe the effects of an experimental application of dilbit on free-living Rhinoceros Auklets.

Chapter 2. Effects of diluted bitumen exposure on reproductive success, flight and diving behaviour of free-living Rhinoceros Auklets (*Cerorhinca monocerata*)

2.1. Introduction

Seabirds' particular vulnerability to oil makes them useful 'sentinal' species and monitoring tools for oil pollution (Camphuysen & Heubeck 2001; King *et al.* 2021). Seabirds are some of the most visibly affected wildlife in the wake of a large oil spill, and constitute a large fraction of observable wildlife mortality (Piatt & Lensink 1989; Munilla *et al.* 2011). Beached bird surveys, which involves routine monitoring of dead birds washed ashore, are useful for monitoring trends in chronic contamination and have a long history of use in Europe (Camphuysen & Heubeck 2001) and North America (Wiese & Ryan 2003; Wilhelm *et al.* 2009). Oil Vulnerability Indices (OVI) are used to score species based on their ecology and spatial distribution to determine which are most at risk from oil, especially in areas of high shipping traffic (Heubeck *et al.* 2003; O'Hanlon *et al.* 2020). More recently, blood, feather, and tissues samples have been used in the long-term monitoring of Yellow-legged Gulls exposed to the 2002 *Prestige* oil spill and have demonstrated their continual exposure to oil-related contamination in the years following the spill (Alonso-Alvarez *et al.* 2007; Pérez *et al.* 2008; Velando *et al.* 2010). There is abundant evidence that oil spills involving conventional oil products (e.g. crude oil) can have acute or long-term effects on seabird's survival rates and breeding success with potential long-term implications for population viability (Eppley & Rubega 1990; Esler *et al.* 2000; Votier *et al.* 2005; Pérez *et al.* 2008)

In contrast to 'conventional' crude oil, in Canada the majority of oil production currently comes from highly viscous oil sands bitumen, which must be diluted in order to enable transport through pipeline. Diluted bitumen (hereafter "dilbit") comprises heavy bituminous crudes and a diluent composed of mainly lighter hydrocarbons such as natural-gas condensates (Dew *et al.* 2015; Ucan-Marin & Dupuis 2015). Canada's reserves of oil sands bitumen, mainly located within the Athabaskan Oil Sands of northern Alberta, is estimated to be around 168 million barrels of currently recoverable product, representing a globally significant fraction of the world's total oil reserves

(Canada 2016). Dilbit is transported via the Trans Mountain Pipeline from the Albertan oil sands to the Westridge Terminal in Burrard Inlet, Vancouver, British Columbia where it is shipped by tanker to overseas destinations (Johannessen *et al.* 2020). The proposed expansions of pipelines and harbor infrastructure to accommodate increased production would result in a sevenfold increase of vessel traffic through the Salish Sea (NEB 2016; Johannessen *et al.* 2020).

Despite the increasing risk of spills and leakages of dilbit into freshwater and marine environments, with increasing pipeline and tanker transport, there is limited research on the risks that this novel contaminant may pose to aquatic fauna. Although there has been extensive research on the effects of conventional crudes on birds and other organisms, dilbit differs from crude oil in its chemical composition and physical characteristics and may therefore have different exposure and toxic effects in the case of a marine spill (Green *et al.* 2017). Chemically, dilbit differs from conventional crudes by having fewer saturates and more resins and asphaltenes (Woods *et al.* 2008; King *et al.* 2015). Its fraction of acutely toxic BTEX (benzene, toluene, ethylbenzene and xylene) monocyclic aromatics occurs in different proportions from crudes, although the specific profile differs depending on the specific blend of dilbit (King *et al.* 2015). These compositional differences result in dilbit having an overall higher viscosity and density and more rapid weathering compared to conventional crude. When released into the environments it may aggregate with sediments and sink, or create free-floating tarballs (King *et al.* 2014; Hua *et al.* 2018; Yang *et al.* 2022). However, its fate in the environment depends on the geographic context of where it was spilled and a variety of dynamic factors including wind, turbulence, salinity, precipitation, tide, and season (King *et al.* 2014; Dew *et al.* 2015; Hua *et al.* 2018; Johannessen *et al.* 2020).

Several reviews have highlighted the lack of research on the toxicity of dilbit, especially on marine fauna (Dew *et al.* 2015; Green *et al.* 2017; King *et al.* 2021). Research shows that, compared with conventional crude, dilbit can exhibit comparable or greater toxicity to embryonic or juvenile fish and benthic invertebrates (Bérubé *et al.* 2021; Schiano Di Lombo *et al.* 2021; Bérubé *et al.* 2023; Indiketi *et al.* 2023; Indiketi *et al.* 2023). These comparative studies suggest that it is not possible to directly extrapolate research on the toxicity of conventional crudes to that of dilbit. There have been limited studies on the effects of dilbit in birds, related to effects on captive passerines and through eggshell contamination (King *et al.* 2022; Ruberg *et al.* 2022).

However, laboratory studies do not necessarily reflect the conditions faced by free-living birds, which also must contend with additional environmental challenges such as variable temperatures, food availability, etc, for survival (King *et al.* 2021).

Rhinoceros Auklets are a species of diving alcid or auk (family Alcidae), closely related to puffins, that breed and winter in the northern Pacific. Nesting pairs construct burrows 1-5m long, and often branching, in which they lay a single egg (Gaston & Dechesne 2020). Rhinoceros Auklets, as diving wing-propelled foragers, are considered to be especially vulnerable to oil spills (Waugh *et al.* 2022). Approximately one fifth of birds killed by the 1986 spill from the *Apex Houston* in California were Rhinoceros Auklets (Carter *et al.* 2003). After the Exxon-Valdez spill in the Gulf of Alaska in 1989, habitat use by Rhinoceros Auklet in nearshore waters of the Kenai peninsula where oil accumulated were initially negatively impacted to the spill but demonstrated recovery by 1991 (Day *et al.* 1997). Lightly oiled auklet carcasses recovered in Japan revealed empty stomachs suggesting starvation as a possible cause of death (Oka & Okuyama 2000).

Here, I used an experimental diluted bitumen exposure to investigate effects on flight and diving behaviour and overall reproductive success in free-living Rhinoceros Auklets (*Cerorhinca monocerata*). Birds were exposed to dilbit either internally – by gavage – or externally on the upper wing coverts and breast feathers. Movement behaviour was obtained using GPS-accelerometers deployed on chick-rearing birds. Specifically the objectives were to determine effects of dilbit exposure on, (1) deployment success and mass change during deployment in adult birds, (2) chick growth (mass and wing length), (3) foraging trip duration and time spent diving, flying, and swimming during foraging trips, (4) diving behaviour including dive depth and duration, descent rate, overall dynamic body acceleration (ODBA), and body angle (pitch) during the descent phase of diving, and (5) flight dynamics including wing beat frequency, amplitude and ground speed, and location of foraging areas.

2.2. Materials and methods

2.2.1. Study species

Fieldwork was conducted on Middleton Island Marine Biological Station in the Gulf of Alaska (59.4283° N, 146.3300° W) during the summers of 2019 and 2021 in the “Rhino Trail” colony, under permits from SFU Animal Care (#1300B-19) and US Fish and Wildlife Service (#23910). On Middleton Island, colonies are located predominately under salmonberry (*Rubus spectabilis*) and red elderberry (*Sambucus racemosa*) on gentle slopes facing the ocean approximately 500m from shore. Eggs are laid in mid-May through late June after which the egg is incubated by both parents; the mean incubation period is 45 days (Leschner 1976; Wilson 1977). Auklets are nocturnal on the breeding colony, departing and arriving between sunset and sunrise (Gaston & Dechesne 2020).

Rhinoceros Auklet chicks are semi-precocial and downy at hatching, and are initially attended by a parent full time for the first 2-3 days. Once chicks are able to independently thermoregulate both parents will depart from the burrow during the day to forage at sea. Parents provision their chick by delivering multiple prey items carried cross-wise in their bills in a “bill load”. They make a single foraging trip per day; therefore a chick will be provisioned at most twice a day if both parents forage successfully. Chick-rearing auklets on Middleton predominately forage on sandlance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*) and greenlings (*Hexagrammos sp.*), although bill-load composition varies considerably within the season and between years (Cunningham *et al.* 2018). The fledging period averages 51 days.

2.2.2. Burrow Monitoring and Treatment Application

In 2019 and 2021, active Rhinoceros Auklet nesting burrows were identified in mid- to late-May, by looking for signs of bird presence (guano, feathers, nest materials) using a series of access-holes, until an incubated egg was discovered. In order to estimate hatch date, the egg was removed and floated in a small vessel of water, using a protractor to estimate angle of float or a small ruler to estimate approximate amount of float, and then dried and returned to the egg chamber. Using a regression curve from (Sun *et al.* 2020) we estimated the expected day of hatching based on the angle or

height of float. Nest burrow access holes were subsequently covered up, burrows identified with stakes and flagging tape, and the main access hole to the egg chamber was marked with a spray-painted orange rock. Due to imprecision in the estimation of hatching date, we began checking nests for signs of hatching five days before the estimated hatch date. Each nest was checked every other day by reaching into the access hole and checking on the egg until hatching. Although we attempted to minimize disturbance to the birds, not all burrows received an equal number of checks prior to hatching.

When an adult bird was discovered in the nesting burrow attending a chick it was sequentially assigned to one of three treatment groups and removed from the burrow and handled in a small cloth bag. Birds received either an internal dose of dilbit (hereafter Internal birds), an external dose of dilbit (hereafter External birds) or received control dosages. The Internal group was gavaged with a slurry of 4 mL dilbit and 4 mL egg yolk administered by a gavage-tube inserted into the esophagus and a 10 mL syringe and received a control application of water on the upper wing coverts and breast feathers. We were unable to administer a precise mL/kg dosage in the field, but for an average 500 g the dosage would be 8 mL/kg. The externally-dosed group was gavaged with a slurry of 4 mL vegetable oil and 4 mL egg yolk, and painted on the upper wing coverts and breast feathers with dilbit. For all external applications, we used a piece of cardboard with a 2x3 cm cutout to standardize the affected surface area. Excess dilbit was removed with a paper towel so that it would not transfer onto other surfaces within the burrow. Control birds were gavaged with a slurry of vegetable oil and egg yolk and stroked with water.

2.2.3. GPS and accelerometer deployment

To track foraging and diving behaviour, GPS-accelerometers (9 g or 1.8% of body mass, AXYTREK, Technosmart, Pisa, Italy) were deployed on all birds. Loggers were programmed to record acceleration in 3 axes (heave, surge and sway) at 50 Hz, depth at a resolution of 0.1m and a rate of 1 Hz, temperature at a rate of 1 Hz, and GPS coordinates every three minutes. We attached the device to a small bundle of central back feathers using a combination of zip-ties, TESA tape and superglue. Devices were designed to fall off after a few weeks in the event of non-recapture. Although similar tags have had behavioral effects on other species of seabirds, all birds in different treatments

in our study were expected to have the same general tag effects. All birds received a metal US Fish and Wildlife band around the tarsus and body mass was recorded (± 1 g) using a 1000-g Pesola spring scale.

Recapture of adult birds took place at night (22:00-3:00) 48 hours after deployment. Burrows were checked every 30 minutes, and when the bird was encountered it was removed from the burrow to retrieve the device. If the bird was not recaptured after three nights of checks, retrieval attempts were halted in order to avoid disruption of the treatment bird's partner.

After deployments, burrows were monitored to determine the fate of the chick. Chicks were measured twice between 5 and 25 days old to obtain a linear growth curve. Chicks were weighed in a bird bag using a Pesola spring scale (± 1 g) and unflattened wing chord was measured (± 1 mm). At 45 days post-hatching burrows were checked for chicks to determine fledging. A chick was considered to be fledged if it was at least 50 days old and no longer present in the burrow.

2.2.4. Analysis of GPS/accelerometer data

In order to reduce the effects of drift in the pressure sensor, zero-offset correction was applied to depth measurements using a two-step filtering process (Luque & Fried 2011). The first smoothing filter calculated a rolling average over a 9 second window to reduce noise. A second filter calculated a rolling average over a moving window of one hour, applied to depths of 0-1m in order to capture the surface signal. Zero-offset values from the second filter were then subtracted from the initial measurements. Dives data used in our analyses were restricted to those that surpassed <2 m depth after zero-offset correction, to ensure that dives were for foraging purposes (Cunningham *et al.* 2018). Dives were split into three phases: descent, bottom, and ascent. The "descent" phase was defined as depths preceding the first recorded local minimum, and the "ascent" phase was defined as depths after the last local minimum. The "bottom" phase was defined as points between the first and last local minima.

For accelerometer-derived metrics, wing-beat metrics were calculated in the Z-axis over a 5-second moving window (Patterson *et al.* 2019). For wing-beat metrics of flapping flight, we focused on wing-beat frequency (WBF) and wing-beat amplitude

(WBA), which are the main factors that give a measure of aerodynamic power output (Krishnan *et al.* 2022). Wing-beat frequency is the number of flaps per second (Hz). Wing-beat amplitude, also called wing-beat strength, is the amplitude of the acceleration signal in the vertical axis (in units of $g = 9.81 \text{ m/s}^2$) during flight, and for a periodic signal will be proportional to the amplitude of body movement (Sakamoto *et al.* 2009; Usherwood *et al.* 2011; Bishop *et al.* 2015; Collins *et al.* 2020; Van Walsum *et al.* 2020). When confined to the same behaviour (e.g. flying or diving), these metrics should provide an assessment of relative intensity of periodic movement and therefore power output (Sakamoto *et al.* 2009; Krishnan *et al.* 2022).

Flapping birds exhibit periodic movement along their dorsoventral (Z) axis during locomotion, whether they are flying or diving (Pennycuik 1990). Discrete Fourier Analysis is used to break up periodic data into a spectrum of component frequencies. We used a Fast-Fourier Transform (FFT) from the package “fft” in base R, performed on the Z-axis acceleration using a 5-second rolling window. We classified WBF as the dominant frequency (i.e., the frequency corresponding to the largest Fourier component). For WBA, identifying the amplitude with the Fourier coefficient of the dominant frequency,

$$A = |X_{\text{dominant}}|, \quad (1)$$

is not a suitable proxy for power output, because there could be several similarly sized components across other frequencies. While the amplitudes of the component frequencies are not purely additive, their energy should be. Borrowing from signal processing, the energy of a signal is defined as:

$$E = \int |x(t)|^2 dt \quad (2)$$

This definition of energy is directly proportional to physical energy. Using Parseval's theorem, which states that the result of the Fourier transform is unitary, this can be expressed as:

$$E = \frac{1}{2\pi} \int |X\omega|^2 d\omega. \quad (3)$$

For a normalized discrete Fourier transform the corresponding expression is:

$$E = \frac{1}{N} \sum_{i=1}^N |X_i|^2, \quad (4)$$

where X_i are the complex Fourier coefficients and N is the length of the signal (in this case the length of the FFT window). In analogy to this, we define the amplitude as

$$A = \sqrt{\sum_{i=1}^N |X_i|^2} \quad (5)$$

to account for the contribution of non-dominant components while preserving the proportionality to energy. In the case of a single-component signal, equation (5) reduces to equation (1) as expected.

Pitch, the vertical angle of the bird with respect to the horizon in degrees, was based on the static acceleration of all three axes, and calculated using the equation

$$\arctan\left(\frac{S_x}{\sqrt{S_y^2 + S_z^2}}\right) \frac{180}{\pi}. \quad (6)$$

Overall dynamic body acceleration (ODBA) was calculated as the sum of the absolute value of all three dynamic components. Dynamic body acceleration was determined in each axis by removing the static (residual) component due to gravity, calculated over a two-second rolling window:

$$ODBA = \left| \frac{\sum X}{n} - X \right| + \left| \frac{\sum Y}{n} - Y \right| + \left| \frac{\sum Z}{n} - Z \right| \quad (7)$$

where n is the length of the rolling window. We used the standard deviation of ODBA calculated over two seconds to reduce noise (Shepard *et al.* 2008).

We classified behaviour into four broad categories: flying, diving, swimming, and at-colony attendance using a stepwise method based on Collins *et al.* (2015) and Patterson *et al.* (2019) (Collins *et al.* 2015; Patterson *et al.* 2019). Behaviours were assigned to each second of accelerometer data, using depth, ODBA, WBF and temperature. Once a data point was classified, it was removed from consideration from subsequent classifications. We first classified “diving” based on depth using a threshold

of 0.5m. We then classified “flying” by identifying periods of high periodicity in the vertical axis of movement by examining the breakpoint in the WBF histogram (Patterson *et al.* 2019). Methods for separating colony attendance and swimming based on pitch and ODBA as in (Patterson *et al.* 2019) were not effective for our data, perhaps because the body angle of Rhinoceros Auklets while swimming versus resting is too similar. Periods of colony attendance were instead determined by visually identifying long (1-3 hours) periods of nighttime behaviour characterized by nonfluctuating warmer temperatures (>25°C), which indicated that the bird had entered its burrow. These periods were bounded by short bouts of flight confirming that this represented ‘colony attendance’.

2.2.5. Statistical analysis

All analysis were conducted in R version 4.1.1 (R Core Team, 2021). Values are reported as means \pm SD throughout, unless otherwise stated, with $P < 0.05$ for significance.

Adult and chick mass, and chick wing, data were analysed using linear mixed-effects models (lmer), with calculation of marginal means (emmeans), and pairwise contrasts, with the trait of interest as the dependent variable, treatment as the main effect and year as a random factor. Chick survival (0/1) was analysed using generalized linear mixed-effects models with binomial distribution [and "logit" link].

Activity during foraging trips was analysed with linear mixed-effects models with treatment as the main effect and tag and year as random factors, with post-hoc pairwise contrasts of marginal means or Kruskal-Wallis tests. We compared diving behavior for day versus night using Student T-tests and subsequently analysed them as separate categories. Dive depth and dive time for individual dives was analyzed using linear mixed-effects models with treatment as the main effect and tag as a random factor.

For flights, we included only flights longer than 5 minutes in duration. We excluded the first “takeoff” minute of the flight. Wing-beat frequency, wing-beat amplitude and ground speed were analyzed using linear-mixed effects models with treatment as the main effect and tag as a random factor.

2.3. Results

2.3.1. Deployment success and mass change during deployment

A total of $n = 22$ GPS-accelerometers were deployed and retrieved with usable data, providing data on $n = 41$ foraging trips (see below). In 2019, $n = 127$ burrows were grubbed and monitored, and GPS-accelerometers were deployed on $n = 29$ birds ($n = 10$ Control, $n = 10$ Internal and $n = 9$ External birds). GPS-accelerometers were recovered with usable data from $n = 8$ Control, $n = 6$ Internal and $n = 1$ External birds (overall recovery rate, $15/29 = 58\%$). In 2021, $n = 120$ burrows were monitored, and GPS-accelerometers deployed on $n = 29$ birds ($n = 10$ Control, $n = 10$ Internal, $n = 9$ External). Recovery rate of GPS-accelerometers in 2021 with usable data was much lower than in 2019: $n = 1$ Control, $n = 2$ Internal and $n = 4$ External ($7/29$ or 28%). Four additional devices were retrieved but with no or incomplete data (e.g., due to the device depleting its battery during deployment).

There was no difference in body mass at deployment among adult birds assigned to the respective treatments ($F_{2,53} = 0.095$, $P > 0.90$). For birds where devices were retrieved body mass at deployment was higher (531 ± 38 g) than that for birds where devices were not retrieved (501 ± 25 g; $t_{42,2} = 3.46$, $P < 0.01$). Birds lost an average of 17.9 ± 26 g (range -70 g to $+23$ g) during the deployment period (paired $t_{25} = 3.42$, $P < 0.01$) but mass change did not differ among treatments ($F_{2,23} = 0.27$, $P > 0.75$; **Table 1**). Mass change was negatively related to mass at deployment ($F_{1,20} = 7.71$, $P = 0.01$): birds that were heavier at deployment loss more mass (**Fig. 1**) but there was no interaction between mass change and treatment ($F_{2,20} = 2.87$, $P > 0.05$).

Table 1. Mass change during deployment (g). Values are means \pm standard deviation. Sample size is given in parentheses.

Trait	Control	External	Internal
Mass at deployment (g)	513 ± 27^a (20)	514 ± 35^a (17)	518 ± 41^a (19)
Mass change during deployment (g)	-20.4 ± 24.8^a (10)	-11.4 ± 28.1^a (7)	-20.1 ± 29.6^a (9)

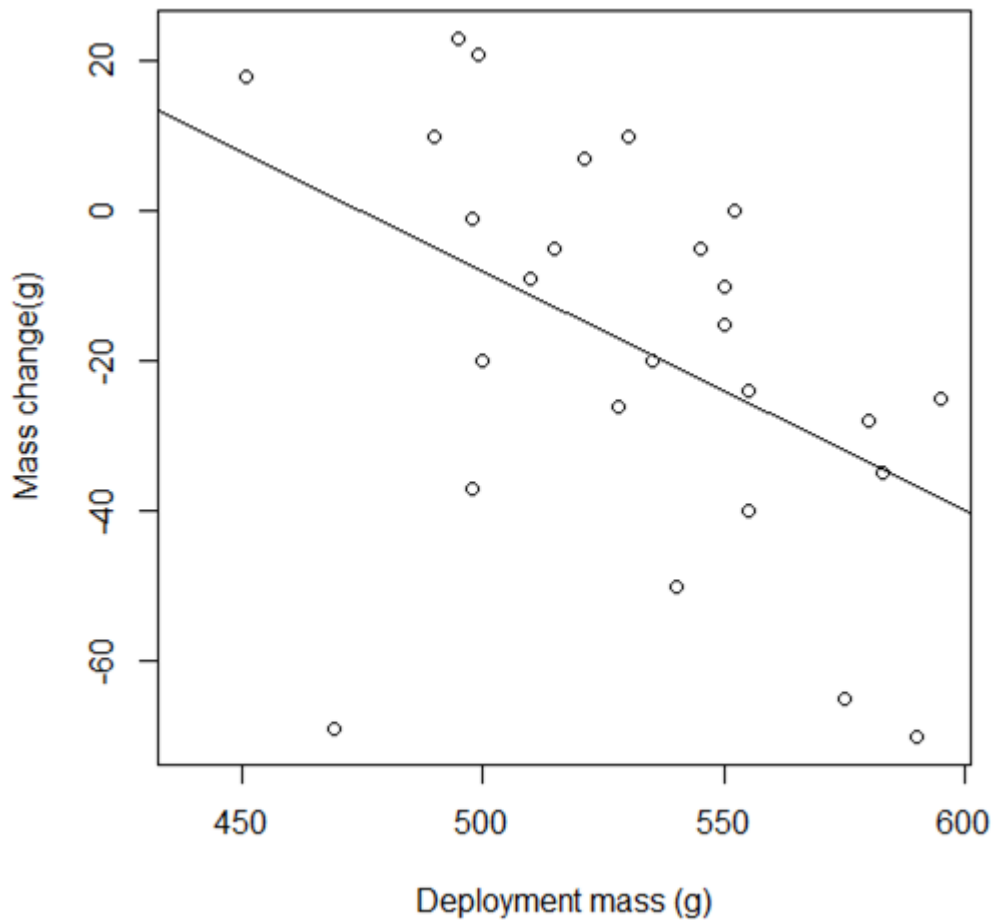


Figure 1. Relationship between initial adult mass (g) and the change in mass during the deployment period.

2.3.2. Effects of treatment on chick growth

Data on chick wing length and body mass at day 5 and day 25 in relation to treatment for individual nests are given in **Appendix 1**. There was no effect of treatment on chick body mass at day 5 ($F_{2,27} = 0.91$, $P > 0.40$) or day 25 ($F_{2,20} = 0.6$, $P > 0.50$; **Table 2**). Similarly, there was no effect of treatment on wing length of chicks at day 5 ($F_{2,25} = 1.6$, $P > 0.21$, controlling for body mass). However, there was an effect of treatment on day 25 wing length ($F_{2,25} = 3.5$, $P = 0.048$, controlling for body mass): chicks of External birds had lower wing lengths than chicks of Control ($P = 0.01$) and Internal birds ($P = 0.06$) birds, with no difference between Control and Internal ($P > 0.50$; Table 2),

Chick growth and survival data for individual nests are presented in **Appendix 1**. Fledging success was independent of treatment ($\chi^2 = 1.14$, $df = 2$, $P = 0.57$; year as a random effect). Fledging success was highest in Internal birds (9/17 nests, 52.9%), lowest in External birds (6/17 nests, 35.3%) and intermediate in Control nests (9/19, 47.3%). However, pooling all treatments fledging success was marginally lower in 2021 (8/25 nests, 32.0%) compared with 2019 (16/28 nests, 57.1%; $\chi^2 = 3.41$, $df = 1$, $P = 0.06$).

Table 2. Chick mass (g) and wing length (mm) at 5 and 25 days old in relation to treatment. Values are means \pm standard deviation; sample sizes are in parentheses

Trait	Age	Control	External	Internal
Mass	5	98.3 \pm 28.1 ^a (12)	84.6 \pm 20.2 ^a (8)	100.9 \pm 30.1 ^a (10)
	25	230.3 \pm 63.0 ^a (12)	197.2 \pm 46.3 ^a (8)	200.7 \pm 56.4 ^a (10)
Wing	5	31.3 \pm 4.7 ^a (12)	26.8 \pm 2.0 ^a (8)	30.9 \pm 6.5 ^a (10)
	25	80.3 \pm 20.0 ^a (9)	59.2 \pm 11.6 ^b (6)	68.6 \pm 22.1 ^a (9)

2.3.3. Effects of dilbit treatment on foraging trips and behaviour

All birds made at least one foraging trip during their deployment (median = 2, max = 4; n = 41 total trips for n = 22 birds). We obtained data for 1 trip from n = 8 birds (36.4%; 4 Control, 3 External, 1 Internal); for 2 trips from n = 10 birds (45.5%, 4 Control, 1 External, 5 Internal), for 3 trips from n = 3 birds (13.6%, 1 Control, 1 External and 1 Internal bird) and 4 trips from n = 1 (4.5%, Internal).

Mean trip length was 26.7 ± 12.3 hours (n = 41). The majority of trips (36/41, 88%) were in the range of 20-27 hours, representing a single day away from the colony. Five trips were longer than one day (44.5-77.5 hours). There was no effect of treatment on trip length (Kruskal Wallis Test, $\chi^2 = 0.02$, df = 2, $P > 0.98$; **Table 3**).

During foraging trips, birds spent on average $19.6 \pm 10.3\%$ of their time diving, $14.2 \pm 6.0\%$ flying, and $66.4 \pm 9.5\%$ swimming. There was a significant, but opposite, effect of treatment on percentage time spent diving ($F_{2,19.0} = 4.34$, $P = 0.028$) and percentage time spent swimming ($F_{2,18.0} = 3.98$, $P = 0.037$), but not on percentage time spent flying ($F_{2,20.2} = 0.02$, $P > 0.90$; Table 3). Internal birds spent less time diving ($P = 0.015$) and more time swimming ($P = 0.019$) compared to External birds. Control birds were intermediate and not significantly different from either treatment group ($P > 0.09$ in all cases; **Table 3 and Fig. 2**).

Table 3. Length of foraging trips (hours) and percentage of time in each activity by treatment. Values are means \pm standard deviation. Sample size is given in parentheses

Trait	Control	External	Internal
Trip length (h)	26.0 ± 11.9^a (15)	28.1 ± 11.1^a (8)	26.6 ± 13.5^a (18)
% time diving	21.1 ± 9.2^{ab} (15)	25.2 ± 13.2^a (8)	15.8 ± 9.1^b (18)
% time flying	14.1 ± 7.2^a (15)	13.9 ± 4.1^a (8)	14.1 ± 6.1^a (18)
% swimming	64.7 ± 9.9^{ab} (15)	60.9 ± 12.1^a (8)	70.1 ± 6.7^a (18)

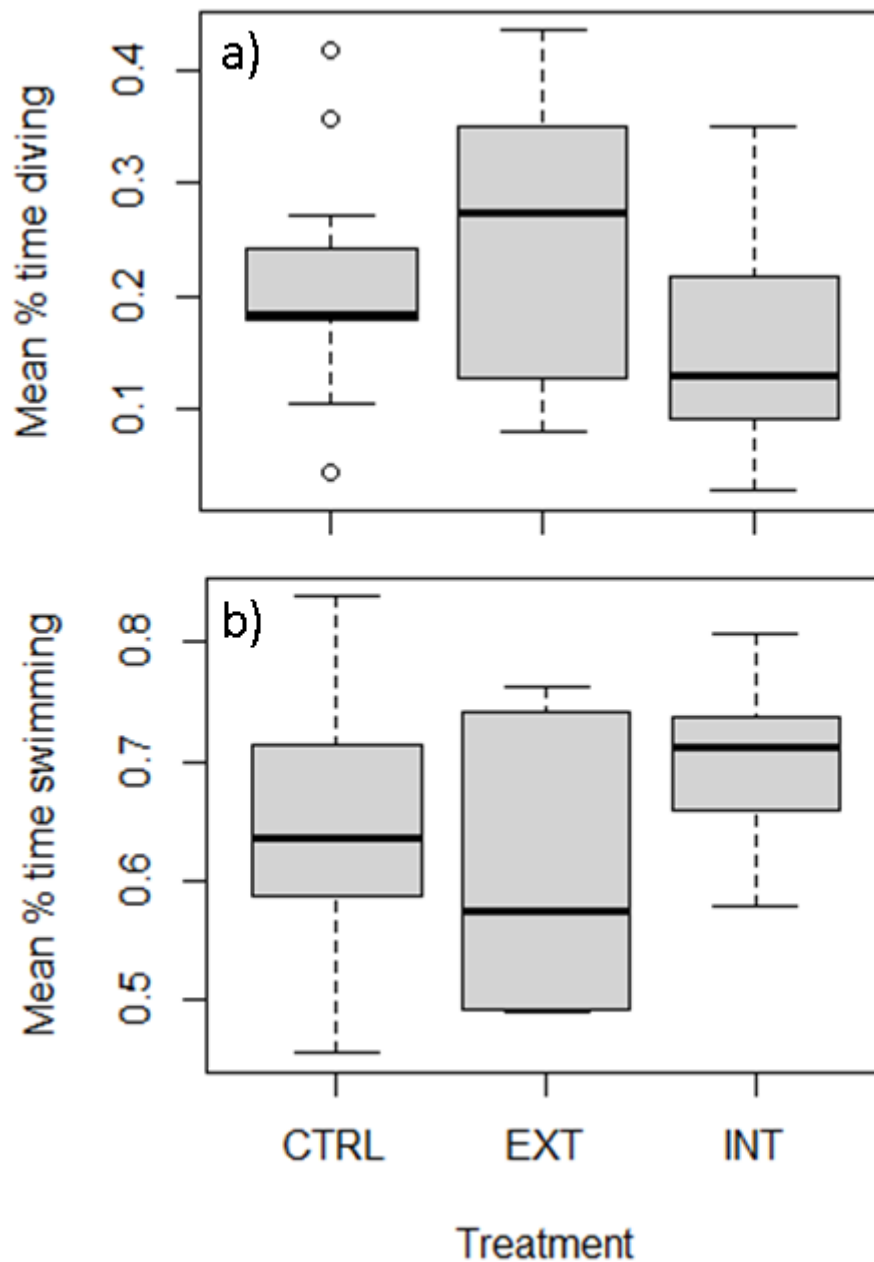


Figure 2. Boxplot with interquartile ranges (IQR) showing variation between treatments in percentage of the foraging trip spent a) diving and b) swimming. Solid horizontal lines are the medians and error bars are the 95% confidence interval. Dots are outliers that lie 1.5 x IQR from the median.

2.3.4. Effects of dilbit treatment on diving behaviour

Birds dove to an average maximum depth of 6.3 ± 3.6 m (max = 40.0 m) with an average maximum dive duration of 40.0 ± 14.3 sec (max = 162 sec, n = total 42,030)

dives). Nighttime dives ($n = 2232$) represented only 5.3% of all dives recorded and were shallower ($t_{3092.4} = 53.1, P < 0.001$) and shorter ($t_{2636.5} = 20.1, P < 0.001$) than daytime dives ($n = 39,798$; **Table 4**; **Fig. 3a,b**). There was no effect of treatment on maximum dive depth either for daytime dives ($F_{2,18.9} = 2.26, P = 0.13$; **Fig. 3a**) or for nighttime dives ($F_{2,15.4} = 0.064, P = 0.94$). Similarly, there was no effect of treatment on maximum dive duration either for daytime dives ($F_{2,18.9} = 0.29, P = 0.75$; **Fig. 3b**) or nighttime dives ($F_{2,15.2} = 1.78, P = 0.20$). Data for individual birds are plotted in **Fig. 4**.

Table 4. Variation in maximum dive depth (m) and dive duration (sec) in relation to treatment for daytime and nighttime dives. Values are means \pm standard deviations; number of dives is in parentheses.

Trait	Time	Control	External	Internal
Maximum dive depth (g)	Day	6.7 \pm 3.5 ^a (13721)	5.5 \pm 2.7 ^a (9097)	6.4 \pm 4.1 ^a (16980)
	Night	3.9 \pm 1.7 ^a (729)	3.4 \pm 1.0 ^a (292)	3.8 \pm 2.4 ^a (1211)
Maximum dive duration (sec)	Day	40.4 \pm 13.7 ^a (13721)	38.6 \pm 14.0 ^a (9097)	40.4 \pm 14.9 ^a (16980)
	Night	33.1 \pm 11.2 ^a (729)	32.3 \pm 12.0 ^a (292)	36.6 \pm 11.3 ^a (1211)

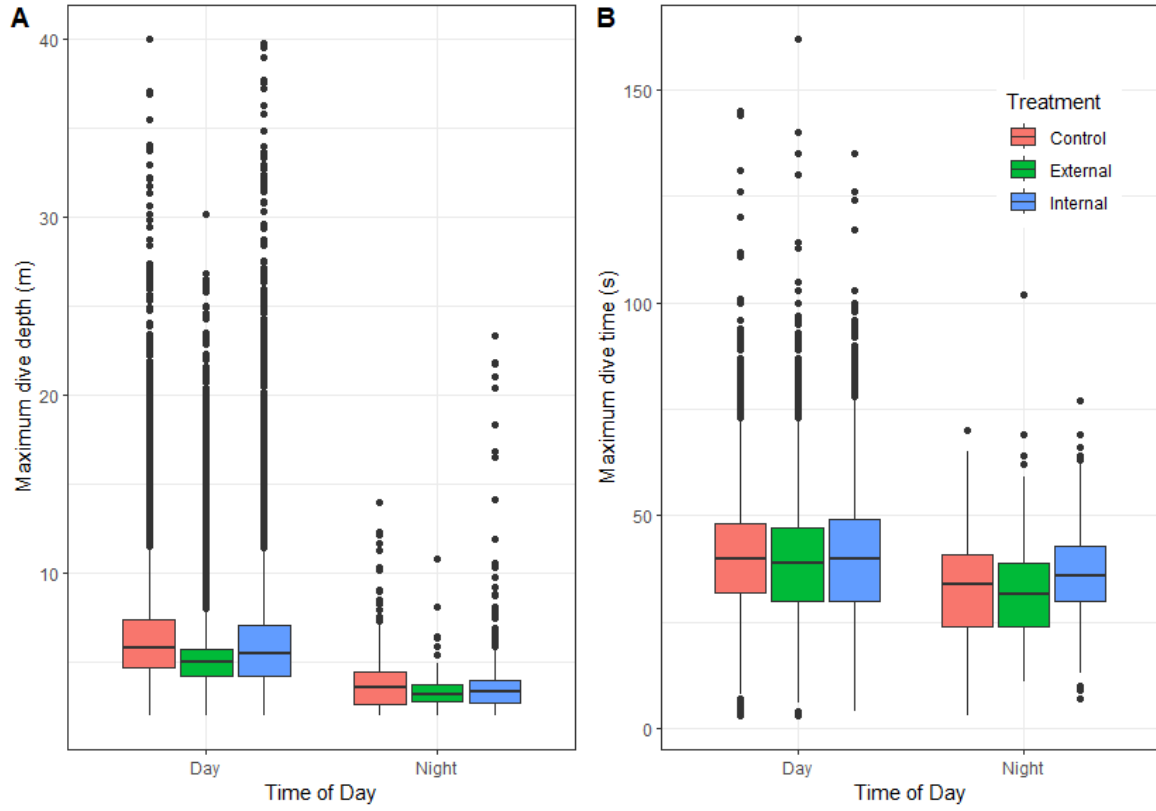


Figure 3. Boxplot with interquartile ranges (IQR) showing variation between treatments and time of day for a) maximum dive depth (m) and b) dive time (sec). Points are outliers that lie 1.5 x IQR from the median.

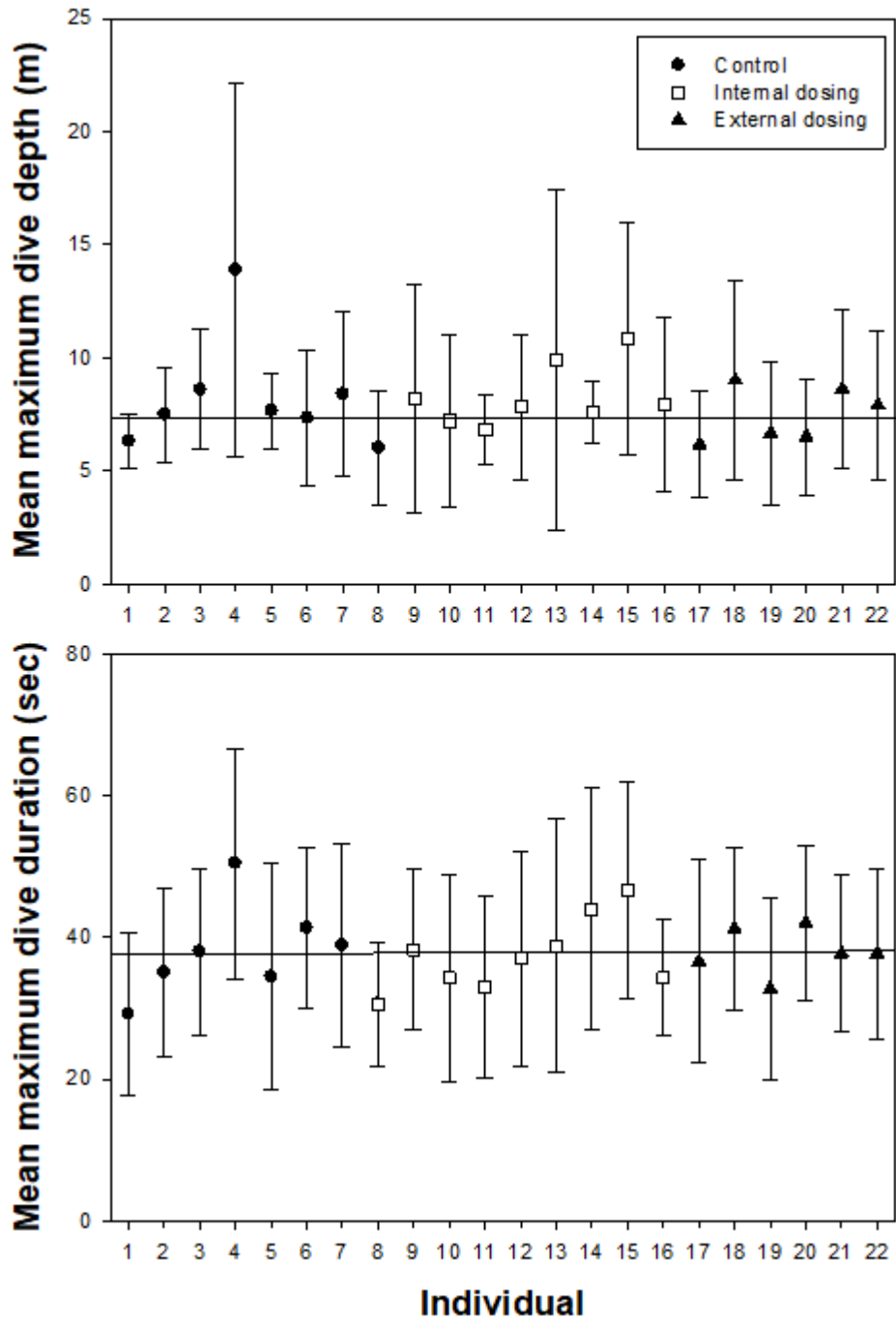


Figure 4. Boxplot with interquartile ranges showing individual variation between (top) mean dive depth and (bottom) mean dive duration for all individuals (n = 22), arranged by dilbit treatment. The horizontal line indicates the overall mean.

For daytime dives, dive depth and dive duration were positively correlated ($r = 0.53$, $P < 0.001$) but there appeared to be an inflection point at ~ 10 m depth (**Fig. 5a**). The slope of the relationship between dive duration and dive depth was steeper for dives < 10 m ($b = 4.04 \pm 0.04$; **Fig. 5b**) compared with dives > 10 m ($b = 1.1 \pm 0.06$; **Fig. 5c**), i.e. relative to dive depth birds spent relatively longer underwater during shallow dives.

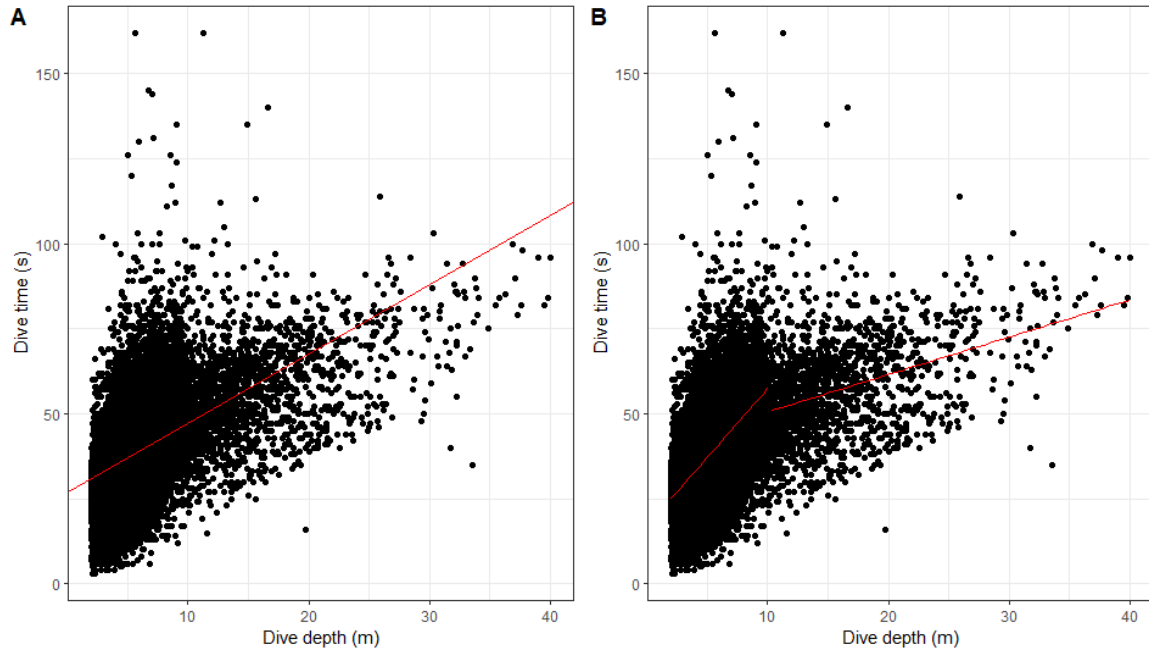


Figure 5. Relationship between dive depth (m) and dive duration (s). Red lines indicate slope b ; in a) slope = 2.04 for all dives, in b) the slope is 4.04 for dives < 10 m depth and 1.1 for dives > 10 m depth. Only daytime dives are included.

Data on a) descent rate and b) ODBA during the descent phase of diving by current depth, binned by 5 m intervals, are given in **Figs. 6, 7 and 8** respectively. Standard deviations overlap substantially among treatments in all cases.

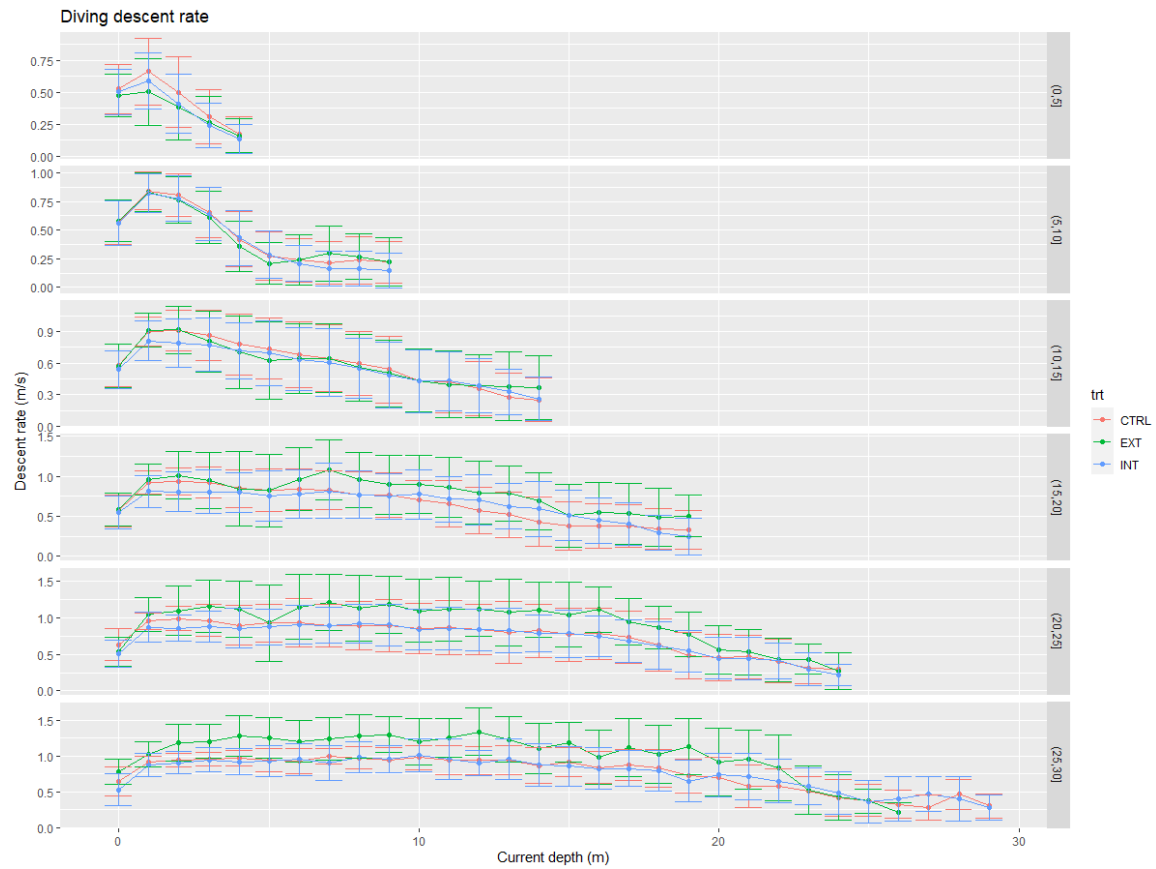


Figure 6. Descent rate (m/s) during the descent phase of diving by current depth. Dives are binned by 5m intervals by the maximum depth achieved during the dive. Error bars are one standard deviation.

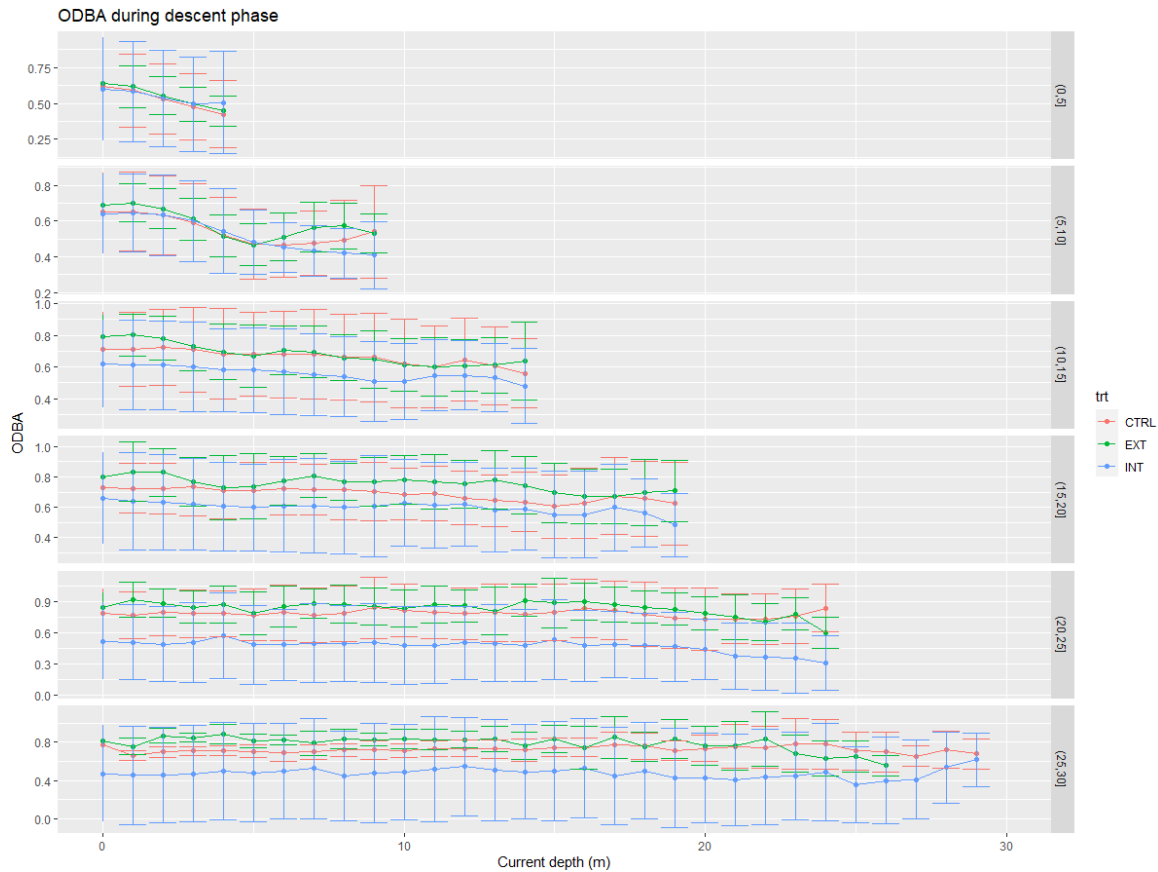


Figure 7. ODBA during the descent phase of diving by current depth. Dives are binned by 5m intervals by maximum depth achieved during the dive. Error bars are one standard deviation.

2.3.5. Effects of dilbit treatment on flying behaviour

There was no effect of treatment on wing beat frequency ($F_{2,19.0} = 0.056$, $P = 0.95$), wing beat amplitude ($F_{2,18.5} = 0.32$, $P = 0.73$) or ground speed ($F_{2,9.9} = 0.43$, $P = 0.66$) for ‘commuting’ flights, excluding the first 60 seconds of take off (**Table 5; Fig. 8**). Data suggested that initial wing beat frequency differed among treatments in the first ~10 seconds after take-off – being highest in Internal birds (**Fig. 9**) – although there was no significant treatment effect at any time interval ($P > 0.05$). All birds regardless of treatment foraged north-west of Middleton Island in coastal waters around Montague Island (**Fig. 11**), a round-trip distance of ~180 km.

Table 5. Variation in wing-beat frequency (Hz), wing-beat amplitude (G) and ground speed (km/hr) during commuting flights in relation to dilbit treatments. Values are means \pm standard deviations. Number of seconds spent is in parentheses.

Trait	Control	External	Internal
Wing beat frequency (Hz)	9.0 \pm 0.6 ^a (115857)	9.0 \pm 0.5 ^a (67252)	9.0 \pm 0.5 ^a (177797)
Wing beat amplitude (g)	142.5 \pm 71.2 ^a (115857)	164.1 \pm 87.3 ^a (67252)	150.6 \pm 77.7 ^a (177797)
Ground speed (km/hr)	50.4 \pm 14.1 ^a (92419)	48.9 \pm 14.4 ^a (61626)	49.8 \pm 10.3 ^a (33065)

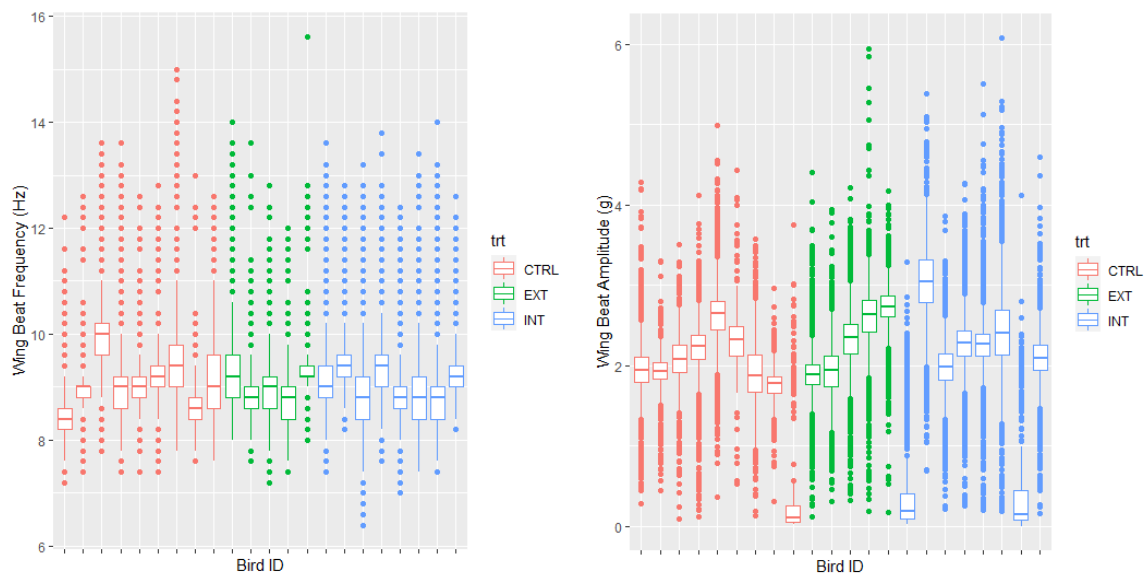


Figure 8. Boxplot with interquartile ranges (IQR) showing individual variation between all individuals (n = 22), for (left) Mean wing-beat frequency (Hz) and (right) amplitude (G) during commuting flights. Solid points represent outliers that are 1.5 x IQR away from the median.

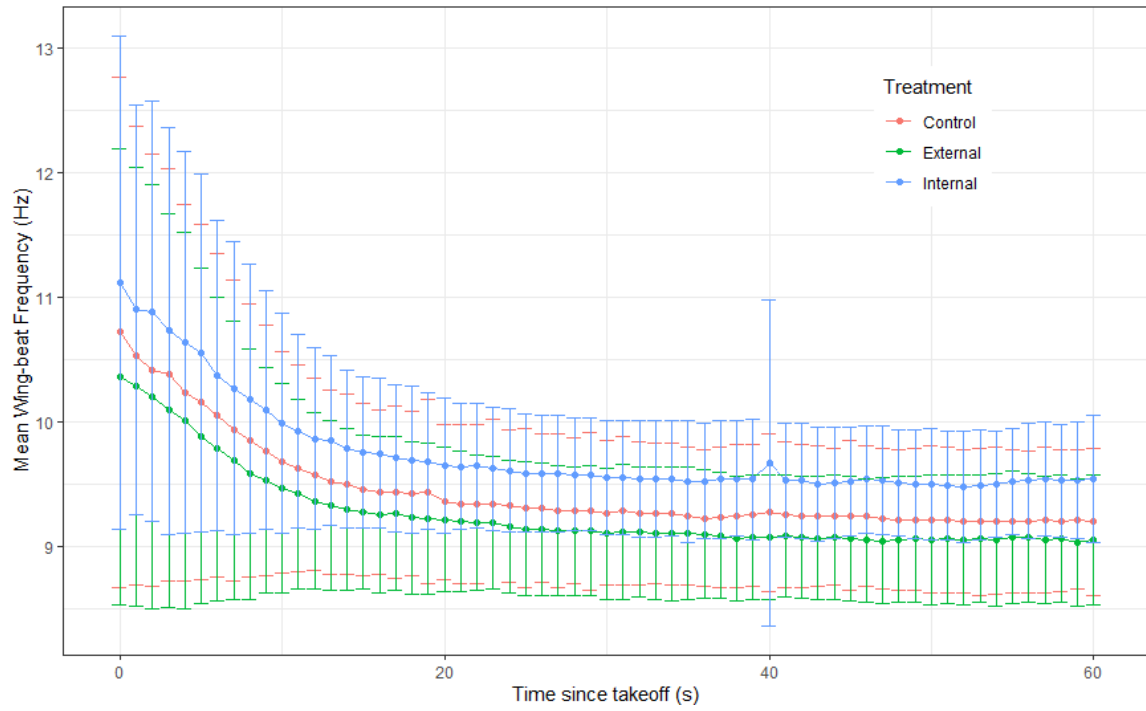


Figure 9. Mean wing-beat frequency (Hz) by flight time (sec) for the first minute of flight, including the takeoff period. Error bars represent one standard deviation.

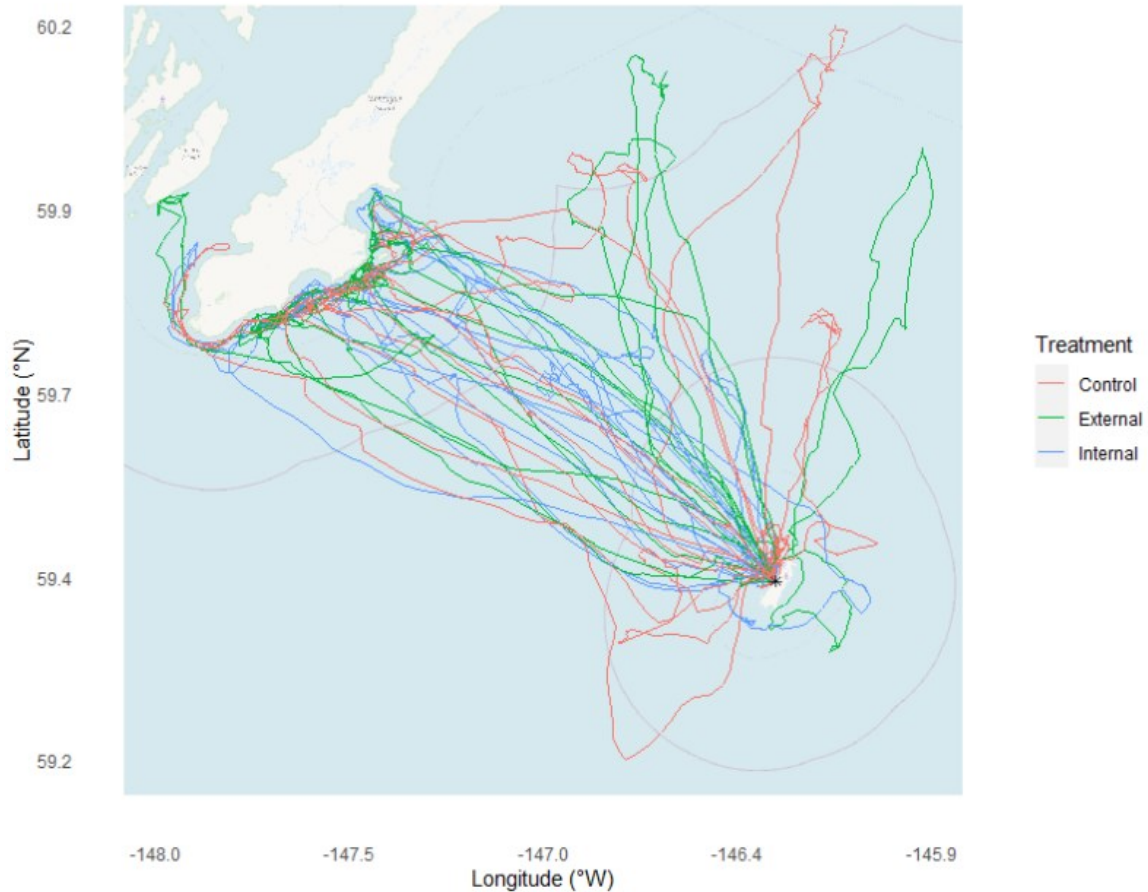


Figure 10. Foraging tracks for Rhinoceros Auklets for both years of deployments (n = 22). Colours represent treatments, star denotes the colony on Middleton Island. Birds mainly foraged in the nearshore waters of Montague Island, although some birds foraged in pelagic waters north of the colony.

2.4. Discussion

2.4.1. Deployment success and tag effects

We recovered a total of 22/58 (37%) GPS-accelerometers which was lower than the rate of retrieval of 67.7% from (Sun *et al.* 2020), who also deployed devices of a similar mass on Rhinoceros Auklets on Middleton Island during early chick-rearing. One difference between these studies is that we had a higher degree of researcher presence on the colony due to deploying a larger number of devices simultaneously within the colony, necessitating more nocturnal checks over a larger area. This excess disturbance might be related to the increased amount of abandonment, suggesting that researchers should also consider indirect disturbance in addition to handling effects when

deploying devices in this colony. (Kato *et al.* 2003) also suggested that researcher presence on the colony at night when auklets are returning to their burrows may be an important source of disturbance. Another key difference from the earlier study is that our handling times were longer due to administering the oral and external treatments. (Sun *et al.* 2020) investigated the effects of handling intensity and found that it was not a factor in abandonment rates. However, the application of treatments in our study, particularly the oral gavage, might have been a substantial additional stressor to the birds contributing to lower recovery rates.

In our study, the recovery rate in 2021 was also significantly lower than in 2019 (28% vs 58%). In 2021, harsher weather, including high precipitation and wind, complicated both tagging and retrieval efforts and possibly contributed to excess stress during handling and during the deployment. In 2021 many non-tagged burrows in the colony suffered flooding and chick death, and so natural rates of abandonment may have been higher. In support of this, the nearby Tower Colony had less flooding in 2021 and abandonment rates did not differ between years.

Birds lost an average of 17.9 ± 26 g of body mass during deployment in our study, but there was significant variability among individuals. This is significantly higher than other studies that deployed similar back-mounted devices to chick-rearing Rhinoceros Auklets on Teuri Island, Japan, which reported mass losses of 1.1 g/day (Kato *et al.* 2003) and 1.4 g/day (Kuroki *et al.* 2003). Many species of alcid lose mass between incubation and chick-rearing (Gaston & Jones 1989; Croll *et al.* 1991), including Rhinoceros Auklets which mainly lose their mass through skin lipids (Niizuma *et al.* 2002). Gaston and Penn (1993) measured mass losses of 44-80 g (4-8% of mass assuming a 1000 g bird) in breeding Thick-billed Murres in less than four days after chick hatching, which is similar to the degree of mass loss observed within our study. It is possible that the greater mass changes we observed compared to studies conducted during later chick-rearing were due to the timing of our deployments (just after hatching). In summary, tag deployment in our study had relatively little effect on adult body mass, for birds that were recovered. However, devices were more likely to be retrieved from individuals that weighed more at deployment. Higher mass could represent birds in better condition, or it could be related to sex differences as males are generally heavier than females (Niizuma *et al.* 2002).

2.4.2. Treatment effects on chick growth

Although there was no difference in chick growth by day 5 for either treatment, External birds had chicks with smaller wing development by day 25. This is contrary to (Trivelpiece *et al.* 1984), who found that Leach's Storm-Petrel (*Hydrobates leucorhous*) chicks whose parents received a single 2.5 ml/kg oral dose of crude oil had decreased survival and reduced mass gain throughout a 21-day study. We did not know the sex of the nestlings in this study, however Sears and Hatch (2008) did not find that nestling sex was a significant factor when measuring mass increase or wing length in Rhinoceros Auklet chicks. Rhinoceros Auklet chicks that receive less food in early development have reduced skeletal development (Sears & Hatch 2008). Therefore, even a single small disturbance to the parent such as encountering a spill can have long-term impacts on fitness. If the effects of external oiling manifest over period of weeks, this could explain the fact that the effects were only visible by day 25.

Although the impact of external oiling on behaviour was not detectable by our accelerometry analyses (see below), the cumulative effects nevertheless could have cause lowered foraging successes and therefore decreased chick growth. Penguins that had been minimally oiled after an oil spill had elevated levels of corticosterone (Fowler *et al.* 1995), which is associated with reduced provisioning rates in other seabirds (Kidawa *et al.* 2017).

2.4.3. Treatment effects on foraging trip duration and overall activity

We found no effect of treatment on foraging trip length. Time-partitioning studies as they relate to oil exposure are rare, making these results difficult to interpret. While oiling studies on homing pigeons (*Columba livia*) showed that oiled birds took more rests and used less efficient flight routes than controls (Perez *et al.* 2017a; Perez *et al.* 2017b), the variability in routes and destinations taken by auklets during our study did not allow for quantitative comparisons between control and treatment birds. Gillies *et al.* (2020) found that handicapped Manx shearwaters (*Puffinus puffinus*) spent less time flying and took longer foraging trips. Rhinoceros Auklets are unable to regulate provisioning rates in response to external pressures (Takahashi *et al.* 1999) and so trip time is perhaps not a useful metric to examine.

In our study, Internal birds spent less time diving and more time swimming compared to External birds, but neither treatment was significantly different from the control group. (Ruberg *et al.* 2022) also found that zebra finches that had been received a low (2 mL/kg/d) oral dose of dilbit spend were more likely to be foraging or in a sleeping posture, and less likely to be “idle” (at rest but alert) after 6 days, although they found no effect on the behaviour of birds moderately dosed (6-8 mL/kg/d) compared to controls. In our study, there was a trend for External birds to spend more time diving, perhaps indicating a need to spend more effort foraging within a single trip. This is compatible with a decrease in foraging efficiency due to the treatment. Alternatively, if External birds were suffering from decreased thermoregulatory ability due to oiling, it may represent increased self-feeding to compensate for the increase in metabolism. Cunningham *et al.* (2017) also found that experimentally externally-oiled cormorants increased their food consumption over control birds, compared to orally dosed birds which lowered their food consumption.

It is also possible that there may have been finer scale differences in behaviour not captured by our coarse categorization. Birds that were not flying or diving while away from the colony were categorized as “swimming” i.e. floating on the water, but this does not necessarily mean that they were at rest. External birds could have devoted more time to preening immediately after oiling as (Ruberg *et al.* 2022), and preening is energetically costly compared to swimming (Enstipp *et al.* 2015). It should be noted, however, that following an experimental release of oil, (Loretsen & Anker-Nilssen 1993) noted that Fulmars did not seem to increase preening in response to becoming minimally oiled.

2.4.4. Treatment effects on diving behaviour

There was no effect of treatment on diving behaviour based on the metrics examined (maximum dive depth and duration, descent rate, ODBA, and body angle). There was marked individual variation but with little consistency among individuals within treatments. This is contrary to our expectations, as the effects of oil on buoyancy are expected to be considerable (O’Hara & Morandin 2010; Morandin & O’Hara 2014; Matcott *et al.* 2019; King *et al.* 2021). Elliott *et al.* (2007) found that Thick-Billed Murres fitted with devices to either increase or decrease buoyancy chose to make shallower, shorter dives. Rhinoceros Auklets experience the greatest resistance from buoyancy in

the first 5 m of their dive and attain neutral buoyancy at 40-60 m (Watanuki & Sato 2008). Both control and treatment birds chose to dive at depths much shallower than their neutral buoyancy. The shallower range of depths in our study may have precluded any differences between treatments.

Auklets dove to an average maximum depth of 6.3 ± 3.6 m and attained a maximum depth of 40 m. These depths are shallower than the averages of 9.2 ± 6.7 reported from chick-rearing birds previously at Middleton Island (9.2 ± 6.7 m: Cunningham *et al.* 2018) and Japan (14.0 ± 1.8 m: Kuroki *et al.* 2003). The average dive duration of 40.0 ± 14.3 sec (max = 162 sec) was within the range observed previously at Middleton (39.2 ± 25.1 sec: Cunningham *et al.* 2018), Seabird Rocks, BC (37.9 ± 1.4 sec & 36.5 ± 1.2 sec: (Davoren 2000), and Japan (53.9 ± 8 sec: Kuroki *et al.* 2003). Dive profiles were mainly V-shaped, suggesting that birds in our study were foraging mainly on small epipelagic schooling fish (Benvenuti *et al.* 2001; Kuroki *et al.* 2003) which is consistent with the main prey items delivered to young chicks at Middleton (predominantly juvenile greenling and sandlance).

Another possibility for the lack of observable effects of treatment on diving behaviour is that the single application of oil to the external feathers of the birds did not disrupt the plumage structure sufficiently to induce a measurable change in buoyancy or drag. However, as sheens of oil as thin as $3 \mu\text{m}$ are able to disrupt feather structure (O'Hara & Morandin 2010; Morandin & O'Hara 2014; Matcott *et al.* 2019), it is unlikely that feathers in our study were unaffected by the treatment. Oka & Okuyama (2000), found that the carcasses of oiled Rhinoceros Auklets were universally emaciated, suggesting that starvation could have occurred from either a) reduced foraging success due to the physical handicaps of oiling or b) loss of waterproofing and subsequent elevated metabolic rate. Given that we found no effects on drag or buoyancy, this supports the hypothesis that loss of waterproofing, hypothermia, and subsequent starvation is the mechanism by which small amounts of external oiling kills birds.

2.4.5. Treatment effects on flight dynamics

Prior research studying the sublethal effects of externally applied crude oil (Perez *et al.* 2017a) and dilbit (Maggini, Kennedy, Macmillan, *et al.* 2017; Maggini, Kennedy, Elliott, *et al.* 2017) on flight dynamics found that oiled birds had reduced wing-beat

power during both takeoff and sustained flight, and took less efficient routes during commuting flights. Despite this, we found no differences between treatments on flight behaviour of rhinoceros auklets in our study based on the metrics examined (wing-beat frequency, wing-beat amplitude or ground speed). One possible reason is that prior studies applied oil to the primaries and tail, which is more likely to affect lift generated by flapping, whereas our application of oil to 5% coverage of body feathers may have caused an amount of drag that was undetectable through our analyses. Krishnan *et al.* (2022) found relationships between wing-beat frequency, wing-beat amplitude, and airspeed in studies of homing pigeons in wind tunnels but not in free-roaming flights, and suggested that wingbeat kinematics in the wild may differ from laboratory wind tunnel observations. Furthermore, due to the challenges of deploying devices on free-living birds we were unable to implement a before-and-after comparison, so the large degree of individual variation observed may have masked any small-scale changes. We did, however, find that Auklets during commuting flight had wingbeat frequencies within the range of 9-13 Hz as determined by (Kuroki *et al.* 2003) using video analysis for all birds, suggesting that neither control or treatment birds differed substantially from normal behaviour.

2.4.6. Effectiveness of treatment in light of few significant results

Although many lab-based studies and field observations demonstrate the many negative effects of crude oil on birds, we did not find many significant results in relation to dilbit dosing. In a review on the effects of petroleum exposure on birds, (King *et al.* 2021) highlights the need to identify environmentally relevant dosages. Our study used a single 8 mL/kg oral dose, over twice that of the 3.3 mL/kg identified by (Hartung 1963) as the amount an oiled mallard duck would ingest when preened from its plumage and an order of magnitude higher than the estimated 0.14 mL/kg that a bird would receive from ingesting heavily contaminated prey (Hartung 1995, p.199). The internal dosage of dilbit we used (8 mL/kg) was selected based on (Ruberg *et al.* 2022), which found a dosage 8 mL/kg/d over 14 days to be the minimum dose to see sublethal effects including behavioural effects. We took a conservative approach since we were working with wild birds with a novel contaminant, and due to Animal Care considerations, and administered only a single dosage. This may not have been a high enough dose to cause noticeable effects in their behaviour, but a robust range-finding experimental

design is difficult to apply with a large, free-living seabird. Another study using a single 5 g/kg dose of crude oil to adult mallard ducks also found no detectable effects (Stubblefield et al. 1995). Trivelpiece et al. (1984) found hypertrophied nasal and adrenal glands of wild Leach's Storm Petrels administered a single 2.5 mL/kg oral dose, but found no change to liver mass or overall adult mass, suggesting that existing effects may not have been detected using our metrics.

In externally dosed birds, the method of applying oil solely to body feathers may not accurately reflect conditions in the wild. We chose to avoid dosing the primaries and tail feathers, which are more important for thrust and drag, for Animal Care considerations. However, wild birds encountering a spill as a surface sheen or mixed into the water are likely to also become oiled on these feathers. Oka & Okuyama (2000) recovered oiled Rhinoceros Auklets carcasses that had been oiled with a minimum external dosage of 12 g or 10% body area, suggesting that these amounts can be lethal. A study on cormorants (Cunningham *et al.* 2017) that externally applied oil to 20% of body feathers every 3 days found that birds had visibly matted feathers and distressed behaviour including feather plucking. Our dosage was less than the lower limit for the "lightly oiled" category by NOAA, which ranges from 6-20% body coverage; our auklets upon retrieval did not appear visibly oiled and had no visibly disturbed plumage, and the skin was not wetted (however, see (Fallon *et al.* 2020) on the effectiveness of visual examination of oiling). Although multiple studies have demonstrated that feather barbule clumping occurs even when exposed to very thin (~3 µm) oil sheens (O'Hara & Morandin 2010; Morandin & O'Hara 2014; Whitmer *et al.* 2018), it is possible that birds that are free to preen may be able to repair their plumage enough to regulate the impacts on buoyancy or drag.

It is also possible that general effects of tagging masked any effects of the dilbit treatment in our study, although we found no immediate effects on body mass during deployment. The increase of the birds' cross-sectional area from the dorsally-attached GPS-accelerometers induced drag in our study birds (Pennycuick *et al.* 2012). Even minimal increases in frontal areas in wind tunnel studies can increase the drag coefficient by up to 50% due to the disruption of the air flow around the body (Pennycuick *et al.* 2012). For birds that also move through water, a far denser medium than air, this effect is even greater. If the disruption of fluid flow during locomotion caused by the increased area by the devices in our study was substantial, it may have

masked the effects of any oil-induced drag. Interpretation of accelerometry results in our study may also be biased as we can only make statements about the birds that returned to the colony and were recovered. Birds that instead chose to abandon the nests may have been more strongly and measurably affected by the treatment. There was no statistically significant difference in abandonment rates between both treatments and control, however this may simply be due to the uniformly low retrieval rate in 2021.

In comparison to conventional crudes, dilbit has been found to be more toxic to adult zebra finches (Ruberg *et al.* 2022) and less toxic to avian embryos (King *et al.* 2022). Unlike these studies, ours focused on behavioural and reproductive endpoints and found no evidence for toxicity. Based on our data, we are not able to determine the relative impact of dilbit compared to conventional crudes as we did not find an effect and similar studies using conventional crudes have not been done with free-living birds. The typical minimum oral dose resulting in adverse effects is around 5 mL/kg/d for conventional petroleum products with effects appearing over several days (King *et al.* 2021); other studies using small (5 g/kg) single oral doses have found no effects (Stubblefield *et al.* 1995). While 10% oiled body coverage has been found to be enough to cause lethality in Rhinoceros Auklets (Oka & Okuyama 2000), we found no evidence for sublethal effects at 5% body coverage. We, cautiously, suggest that dilbit is then, at least, not more toxic, nor more damaging to plumage structure, than crude oils at small dosages for the endpoints examined in our study.

2.5. Conclusion and implications for dilbit transport in the Salish Sea

We applied GPS-accelerometers to free-living Rhinoceros Auklets to investigate differences between fine-scale behaviour of dosed vs. control birds. We found that chicks raised by External birds had reduced growth. We found small differences in time-activity budgets, with Internal birds spending more time swimming and less time diving compared to External birds. Contrary to our expectations, we found no difference in the flight or diving behaviour of externally dosed Rhinoceros Auklets based on the accelerometer-derived metrics examined, which may suggest that the small scale of the dilbit application was insufficient to cause enough change in buoyancy or drag. This is the first study of the effects of diluted bitumen on adult seabirds, and among the first studies to study the effects of an experimental treatment of a petroleum product on a

free-living seabird. We took an approach that looked at the behaviour of free-living birds to observe the effects of exposure to oil in addition to the challenges of a breeding season. Working with free-living birds presents numerous challenges including a limited ability to closely monitor the bird after deployment and an inability to control various environmental factors such as weather and foraging conditions. Benefits, however, include the ability to see how a free-living bird responds to exposure without the confounding variables of captivity-induced responses. Although there have been several studies investigating the impacts of surface-level applications of oil on flight behaviour in wind tunnels, there has been very little experimentation on its effects on diving despite the fact that diving birds are among those most strongly affected by oil spills (Waugh *et al.* 2022). Similar studies on captive birds, using accelerometers as well as video analysis, could identify the specific aspects of diving impacted by external oil application. Captive studies would also allow for before-after comparisons to better control for individual variation, which can be considerable. We avoided oiling flight feathers out of concerns that the birds' ability to locomote would be overly compromised, but a captive study where birds could be closely monitored and properly cleaned afterwards would not necessarily face such a restriction. Investigating how oiled captive birds react when interacting with surface slicks would also allow for a more realistic identification of an external dose that a bird is likely to impact its thermoregulatory or locomotory abilities. This knowledge would be beneficial should this experiment be repeated with larger sample size so that confounding variables could be better addressed. Future research would also benefit from investigating the effects of dilbit applications on other sublethal physiological endpoints, such as adrenal stress, hemolytic injury, immunotoxicity and histopathological injury.

We used oil that had been weathered by placing it in an open glass jar in ambient temperatures for over 24 hours. The resulting product was extremely viscous and when applied on the bird's contour feathers remained in a thick coating that did not seem to penetrate the inner layer of plumage. However, the physical properties of dilbit (density and viscosity) change in response to a number of factors such as weathering, temperature and salinity. Although oils, including nontoxic edible oils such as fish or vegetable oils, are known to universally disrupt feather structure, it is currently not well understood how differences in viscosity or salinity impact the overall effects of the oil on a living bird. Given that ocean conditions can be variable throughout and within seasons,

these data gaps could be addressed to better understand the risks that a spill may pose to seabirds given the type of oil and current ocean conditions.

Rhinoceros Auklets are present year-round in the Salish Sea, Strait of Juan de Fuca and Puget Sound, including the presence of a large breeding colony on Protection Island, Washington (Gaston & Dechesne 2020). Additionally, other populations of diving and surface-foraging seabirds breed in the region. Increased transportation of diluted bitumen through the Salish Sea will result in an increased risk of spillage. Nevertheless, we found that a small application of oil early in the breeding season resulted in reduced chick growth by day 25; this single event has the potential to damage a chick's lifelong fitness and would have population level effects if the number of affected breeders is sufficiently large. Furthermore, an eggshell-dosing study by (King *et al.* 2022) found that dilbit could be absorbed through eggshell and be absorbed by the embryo, A chick hatching from an egg that has had oil transferred to its shell during incubation must contend not only with the direct toxic effects of the contaminant, but also the effects of being reared by a contaminated parent that may be less capable of foraging. Thus, we suggest that oil tankers avoid seabird colonies and areas that are commonly used for foraging during the breeding season in order to mitigate the damage caused by a spill. In addition to nesting colonies, the Salish Sea supports many populations of wintering seabirds. We did not detect any behavioural or toxicological effects of small applications of oil to free-living adult seabirds, implying that a winter spill may not be as damaging as one in the summer. However, given that our study took place during summer, ocean conditions were warm and we cannot rule out the risk of hypothermia in a winter spill.

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Appendix A. Chick survival and growth rates by year and treatment for all deployments

Year	Treatment	Day 5 survival	Day 5 mass (g)	Day 5 wing (mm)	Day 25 survival	Day 25 mass	Day 25 survival	Fledging success
2019	CTRL	1	79	26	0	.	.	0
2019	CTRL	1	64	24	0	.	.	0
2019	CTRL	1	105	34	1	201	82	1
2019	CTRL	1	120	36	1	260	86	1
2019	CTRL	0	.	.	0	.	.	0
2019	CTRL	1	81	26	1	310	110	1
2019	CTRL	1	131	34	1	287	96	1
2019	CTRL	1	110	37	1	285	93	1
2019	CTRL	1	65	37	1	145	54	1
2019	CTRL	1	125	33	1	260	87	1
2019	EXT	0	.	.	0	.	.	0
2019	EXT	0	.	.	0	.	.	0
2019	EXT	1	85	29	1	120	46	1
2019	EXT	1	110	29	1	265	75	1
2019	EXT	1	79	26	1	195	59	1
2019	EXT	1	75	27	0	.	.	0
2019	EXT	0	.	.	0	.	.	0
2019	EXT	0	.	.	0	.	.	0
2019	EXT	1	75	26	1	208	54	1
2019	INT	0	.	.	0	.	.	0
2019	INT	1	120	31	1	230	76	1
2019	INT	0	.	.	0	.	.	0
2019	INT	0	.	.	0	.	.	0
2019	INT	1	135	45	1	235	94	1
2019	INT	1	120	33	1	230	78	1
2019	INT	1	117	37	1	270	89	1
2019	INT	0	.	.	0	.	.	0
2019	INT	1	54	28	1	155	50	1
2021	CTRL	1	54	26	0	.	.	0
2021	CTRL	0	.	.	0	.	.	0
2021	CTRL	1	113	32	1	169	51	1
2021	CTRL	0	.	.	0	.	.	0
2021	CTRL	0	.	.	0	.	.	0
2021	CTRL	0	.	.	0	.	.	0
2021	CTRL	1	132	31	1	156	64	1

2021	CTRL	0			0			0
2021	CTRL	0			0			0
2021	EXT	0			0			0
2021	EXT	1	112	28	1	193	50	1
2021	EXT	1	50	23	0			0
2021	EXT	1	91	26	1	202	71	1
2021	EXT	0			0			0
2021	EXT	0			0			0
2021	EXT	0			0			0
2021	EXT	0			0			0
2021	INT	1	89	26	1	194	59	1
2021	INT	1	138	31	1	252	91	1
2021	INT	0			0			0
2021	INT	1	88	24	0			0
2021	INT	1	56	23	1	119	32	1
2021	INT	0			0			0
2021	INT	1	92	31	1	121	48	1
2021	INT	0			0			0
