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Experimental and modeled thermoregulatory costs of repeated sublethal oil exposure in the Double-crested Cormorant, *Phalacrocorax auritus*

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ABSTRACT

To fully understand the impact of oil exposure, it is important to understand sublethal effects like how increased thermoregulatory costs may affect survival and reproduction. However, it is difficult and time-consuming to measure these effects in wild animals. We present a novel use of a bioenergetics model, Niche Mapper™, to estimate thermoregulatory impacts of oiling, using data from captive Double-crested Cormorants (*Phalacrocorax auritus*) experimentally exposed to oil. Oiled cormorants had significant increases in surface body temperatures following exposure. Niche Mapper accurately predicted surface temperatures and metabolic rates for unoiled and oiled cormorants and predicted 13–18% increased daily energetic demands due to increased thermoregulatory costs of oiling, consistent with increased food consumption observed in experimentally oiled cormorants. We show that Niche Mapper can provide valuable insight into sublethal oiling effects by quantifying the extent to which thermoregulatory costs divert energy resources away from important life processes like maintenance, reproduction and migration.

1. Introduction

The threat of oil pollution to marine birds is well-documented (e.g., Votier et al., 2005), and can affect marine birds indirectly (e.g., killing or contaminating food sources) or directly. The direct effects of oil exposure stem from the toxicity of ingested oil and adverse effects of plumage oiling, the latter being the focus of this work. Oil exposure compromises the integrity of a bird's feather microstructure by collapsing the interlocking structure of feather elements. This results in feathers matting together, causing the insulative air layer in the plumage to be displaced and a loss of waterproofing (O'Hara and Morandin, 2010). This, in turn, affects the thermal balance of oil-exposed birds that can require additional energetic expenditures to maintain homeothermy.

Experimental studies have documented increased metabolic heat production in response to oiling in several avian species (Table S1). The magnitude of increased heat production is dependent on dosage, environmental temperature, exposure to water, and differences in plumage types among species. At one extreme, heavily oiled birds in cold aquatic environments can die of hypothermia or starvation if unable to feed enough to offset increased energetic requirements (e.g., Oka and Okuyama, 2000). For birds in milder environments or that are less-heavily oiled, the increased energy expenditures following oiling may not be lethal but may still affect fitness by diverting resources away from maintenance, growth, and reproduction.

While large, catastrophic spills that cause immediate mass mortalities garner much of the media and scientific attention, there is growing recognition of the need to better understand the effect of exposure to chronic (low volume) oil discharges (Wiese and Robertson, 2004; Henkel et al., 2014; Fraser and Racine, 2016). A majority of anthropogenic oil pollution comes from chronic discharges from sources like the offshore oil and gas industry, shipping vessels and non-point runoff from land-based activities (O'Hara and Morandin, 2010; Henkel et al., 2014). Chronic exposure can cause mortality in some

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locations (e.g., Wiese and Ryan, 2003), but there are also likely more widespread sublethal effects of such exposures.

To date we are unaware of attempts to model repeated sublethal oil exposure and predict the effects due to increased thermoregulatory costs. Here we present a novel use of a bioenergetics model, Niche Mapper™, to predict the thermoregulatory effect of oil exposure on the Double-crested Cormorant (*Phalacrocorax auritus*; hereafter cormorant), a large, diving waterbird often impacted by oil spills (Dorr et al., 2015). We develop an “oiled' cormorant model by modifying the inputs used by Niche Mapper to calculate body insulation to simulate oil introduced into the plumage. We then test Niche Mapper's ability to accurately model thermoregulation in oiled and unoiled cormorants by comparing predicted surface temperatures and energy expenditures to those measured in captive cormorants experimentally exposed to oil. Mechanistically modeling the thermoregulatory effects of oil exposure allows for simulations of wild animals' energetics to gain a more complete understanding of the effects of oil pollution on wildlife.

2. Methods

2.1. Summary of live cormorant experiments

As part of the Natural Resource Damage Assessment performed in response to the 2010 Deepwater Horizon (DWH) oil spill in the Gulf of Mexico, wild cormorants were captured from Mississippi and Alabama, USA, and transported to captive facilities at the National Wildlife Research Center, Mississippi Field Station (Bursian et al., 2017). The focus of the present work is developing modeling techniques and so we summarize the live bird experiments to provide context. For a detailed description of procedures see Cunningham et al. (2017).

All cormorants were individually housed in 1.5 × 1.5 × 1.8 m cages containing 190-liter plastic water tanks that were refilled daily. Cormorants were offered 600 g of live channel catfish (*Ictalurus punctatus*) daily. All birds had an Advanced Telemetry Systems (ATS, Isanti, MN USA) F1815T very high frequency temperature transmitter surgically implanted in the coelom prior to study initiation to monitor internal body temperature daily (see Scherr, 2009 for details). Cormorants were allowed to acclimate to captivity and recover from surgery for a minimum of 21 days prior to initiation of the oiling study.

Twenty-five cormorants were assigned to control (n = 12) or oiled (n = 13) treatment groups. Seven cormorants had evidence of preexisting illness based on monocyte counts and were assigned randomly between the control and oiled groups (4 and 3 birds respectively). During the course of the trial, one bird from the control group (day 1) and two birds from the oiled group (day 15 and 19) died (Cunningham et al., 2017).

Cormorants in the oiled group were exposed to artificially weathered DWH oil by applying approximately 6.5 g of oil to both the breast and back by brush. The oil was applied across an area accounting for 20% of the total body surface area excluding wings and tail; subsequent preening by the birds further spread the oil. Cormorants in the control group received the same treatment except that oil was replaced with water. Oil or water was applied to the birds every three days through day 16 of the trial (Table S2). Body weight was measured every three days for the duration of the trial and at necropsy.

External body temperature of all cormorants was taken with a handheld scanning thermograph camera (FLIR®) three days prior to day 1 oiling, and every six days thereafter (Table S2). Birds were taken from their cage to an adjacent room where they were held at a standard distance and position for each photo to ensure reproducibility. Temperatures for different body parts were extracted using FLIR® ThermaCAM 342 Researcher Pro 2.7 software. Food intake was calculated based on daily consumption of fish. Visual bird health checks were conducted twice daily (Cunningham et al., 2017).

2.2. Niche Mapper description

Niche Mapper (Porter and Mitchell, 2006) is a bioenergetics model that has been previously shown to accurately predict energetic requirements as a function of environmental conditions and animal morphological and physiological properties for a wide variety of animals, including several waterbirds: cormorants (*Phalacrocorax* sp.), Brünnich's guillemots (*Ura lomvia*), and little auks (*Alle alle*) (Fort et al., 2009, 2011; Göktepe et al., 2012). Niche Mapper consists of two submodels: a microclimate model and an animal model. The microclimate model uses macroclimate data (maximum and minimum daily air temperatures, cloud cover, wind speed, relative humidity), substrate properties, geographic location, and time of year to calculate hourly environmental conditions at the animal's height (see Fuentes and Porter, 2013 for details).

The animal model then uses the hourly outputs from the microclimate model and animal properties to iteratively solve a heat balance equation to find the metabolic rate needed for the animal to maintain its body temperature, accounting for convective, radiative, evaporative, conductive and solar heat fluxes with its microenvironment (see Supplemental materials and Mathewson and Porter, 2013 for details). Most relevant to this work, Niche Mapper calculates animal surface temperatures based on core temperature, physical dimensions, and insulation of the body part in order to compute heat flux with the environment. Thus, the model allows us to explore how altered insulation (e.g., in response to oiling) affects surface temperatures and, ultimately, heat loss to the environment.

We updated the cormorant model used by Göktepe et al. (2012) to a multipart model with truncated cones for the beak and head, cylinders for the neck and legs, and an ellipsoid for the torso (Fig. S1). During diurnal and crepuscular hours, all body parts were exposed to the environment. During nocturnal hours, we assumed no heat loss for the head (tucked under wings) and 30% of the neck (in contact with torso) to simulate birds in a sleeping posture. Key animal model inputs are summarized in Table 1, and the following physiological thermoregulatory options were allowed: vasodilation and vasoconstriction, increasing body temperature, ptiloerection, and gular fluttering. Leg and beak body temperatures were allowed to drop below body temperatures for other body parts to simulate counter-current exchange mechanisms (Fitzpatrick et al., 2015). See Supporting information for additional information on Niche Mapper operation.

2.3. Niche Mapper metabolic chamber simulations

We first evaluated the unoiled cormorant model with a metabolic chamber simulation to compare predicted metabolic rates as a function of air temperature to those reported by Enstipp et al. (2006, 2008). In this simulation, all environmental temperatures (air, ground, and sky) were set to the same value and increased incrementally. We assumed no solar radiation, 5% relative humidity, and wind speeds of 0.1 or 1.0 m/s to account for uncertainty regarding the velocity of the airflow in the experimental metabolic chambers.

We also compared Niche Mapper heat production predictions for cormorants resting on the water surface to those measured by Enstipp et al. (2006) in a metabolic chamber. We simulated cormorants as having their legs fully submerged and 50–90% of their torso submerged. Double-crested Cormorant plumage is partially wettable (Mahoney, 1984). Based on studies by Enstipp et al. (2006) and Grémillet et al. (1998, 2005) on shallowly-submerged Double-crested Cormorant and Great Cormorant (*Phalacrocorax carbo*) carcasses respectively, we assumed water penetration reduced the effective ‘dry’ insulation layer thickness in the model to 2 mm.

2.4. Surface temperature comparisons

For each day that FLIR images were taken of the live cormorants, we