

AN ABSTRACT OF THE THESIS OF

Daniel J. Rizzolo for the degree of Master of Science in Wildlife Science presented on February 5, 2004.

Title: Behavioral Constraints on Harlequin Duck Population Recovery from the Exxon Valdez Oil Spill in Prince William Sound, Alaska.

Abstract approved:

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I investigated the relationship between harlequin duck (*Histrionicus histrionicus*) behavior and lack of recovery from the *Exxon Valdez* oil spill in Prince William Sound, Alaska. First, I evaluated the hypothesis that harlequin ducks in winter have little flexibility to increase foraging time in response to disturbance because they are constrained to forage during daylight. Eight radio-tagged harlequin ducks wintering in Resurrection Bay, Alaska were monitored for evidence of dive-feeding at night. Each radio-tagged individual was detected during an average of 19.5 of 22 nocturnal monitoring sessions and signal loss indicative of diving behavior was not detected during a total of 780 minutes of signal monitoring. In contrast, the same 8 radio-tagged birds were detected during an average of 9.1 of 12 daytime signal monitoring sessions and signal loss

indicated diving behavior during an average of $62 \pm 7\%$ of 5-minute daytime monitoring periods (total of 364 minutes of signal monitoring). Thus the harlequin ducks monitored in this study rarely, if ever, fed by diving at night, possibly due to reduced foraging efficiency and (or) increased predation risk at night. This result suggests that harlequin ducks in mid-winter may be severely time-limited in their foraging, especially in northern parts of their winter range. Therefore, subtle changes in energy requirements and (or) time-activity budgets as a result of continued exposure to residual oil from the *Exxon Valdez* oil spill may affect the ability of harlequin ducks to meet their daily energy requirements.

Second, I tested the hypothesis that exposure to crude oil affects time-activity budgets of harlequin ducks. Controlled oil-dosing and plumage-oiling experiments were conducted using adult female harlequin ducks in captivity. I found no evidence that ingestion of weathered Prudhoe Bay crude oil affected the occurrence of feeding activity during 30-minute observation periods, nor was there evidence of effects on time spent feeding. Effects of crude oil ingestion on maintenance activity were detected, but were neither consistent between the 2 years of the study, nor dose-dependent for the 2 doses administered (2 and $20 \text{ mL kg}^{-1} \text{ wk}^{-1}$), and therefore did not strongly support an oil-dosing effect on maintenance activity. Consequently, these results provided little support for the hypothesis that oil ingestion affects time-activity budgets of captive harlequin ducks, at least for the doses and conditions of captivity used in this study. Plumage-oiling reduced feeding activity in captive harlequin ducks. The estimated probability of feeding

during 30-minute observation periods for birds in the high-exposure oiling group (5 mL of crude oil) was 53% less than that of non-oiled controls. Oiled birds exhibited a trend of reduced time feeding with increasing level of external-oiling; this effect was greatest among birds in the high-exposure oiling group, which spent 43% less time feeding than non-oiled birds. Reduced feeding was associated with less time in the water dive-feeding and presumably lower heat loss. Trends in the occurrence of maintenance activity and time spent in maintenance activity for birds in the high-exposure treatment suggested plumage-oiling increased maintenance activity, but results were not conclusive. The behavioral changes associated with plumage-oiling in captivity would likely reduce fitness in the wild, where a high proportion of time must be spent in the water feeding. If residual *Exxon Valdez* oil sequestered in beach sediments enters the water column where it may be encountered by harlequin ducks, external exposure may lead to reduced feeding activity. This, in turn, may compromise survival, particularly during mid-winter when the time available for diurnal foraging is low and maintenance energy requirements are high.

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Behavioral Constraints on Harlequin Duck Population Recovery from the *Exxon*
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Dr. Daniel Esler acquired funding, assisted with study design, data analysis, interpretation of results, and provided editorial comments for both manuscripts.

Dr. Daniel D. Roby provided input on study design, assisted with interpretation of results, and provided extensive editorial comments for both manuscripts. Dr.

Robert L. Jarvis provided input on study design and editorial comments for both manuscripts.

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Dedicated to Dr. Craig S. Hieber,
an influential teacher whose
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greatly missed.

BEHAVIORAL CONSTRAINTS ON HARLEQUIN DUCK POPULATION
RECOVERY FROM THE *EXXON VALDEZ* OIL SPILL IN
PRINCE WILLIAM SOUND, ALASKA

CHAPTER 1

GENERAL INTRODUCTION

Daniel J. Rizzolo

The grounding of the oil tanker *Exxon Valdez* on Bligh Reef in Prince William Sound (PWS), Alaska, USA in 1989 spilled nearly 42 million liters of Prudhoe Bay crude oil and caused extensive damage to the marine ecosystem (reviewed by Peterson 2001). For marine birds, estimates of acute mortality from the spill were in the hundreds of thousands (Piatt et al. 1990). Despite this large initial loss, populations of many bird species showed remarkable resilience and signs of recovery within a relatively short period of time (Bowman et al. 1995, Wiens et al. 1996). For other species, however, signs of recovery were not as clear. In 1995, the Nearshore Vertebrate Predator project was initiated to examine recovery of the nearshore ecological community by focusing on a suite of vertebrate species that are top-predators in the nearshore community (Holland-Bartels 2002). The weight of evidence produced by this research supported the hypothesis that residual oil trapped in intertidal sediments continued to enter the food web and have negative effects on some invertebrate-feeding predators in PWS (Holland-Bartels 2002). The harlequin duck (*Histrionicus histrionicus*) was among the species determined to have incurred long-term negative effects from the oil spill (Esler et al. 2002).

Both abundance and survival components of harlequin duck winter demography in PWS have shown evidence of oil spill effects as many as 9 years after the spill (Esler et al. 2002). Densities of harlequin ducks in oiled areas during winters 1995 to 1997 were lower than expected after accounting for effects of habitat, prey abundance, and prey biomass (Esler et al. 2000a). Fall population

surveys documented numerical declines in oiled areas over this same period, while numbers on unoiled areas remained stable (Rosenberg and Petrula 1998).

Estimated cumulative winter survival rate for adult female harlequin ducks during this period also was lower in oiled areas compared to unoiled areas, implicating increased mortality as the mechanism underlying differences in abundance between areas (Esler et al. 2000*b*).

Oil contamination has persisted in both the nearshore habitats and intertidal benthic invertebrate communities of heavily oiled areas. Intertidal and shallow subtidal habitats in PWS received 40% of the spilled oil and, of that, 10% was estimated to remain subsumed in the sediment 3 years after the spill (Wolfe et al. 1994). An extensive survey of PWS conducted in 2001 found residual oil at 53 of 91 sites randomly selected from those classified as heavily- or moderately-oiled following the spill (Short et al. 2004). This subsurface oil was still liquid, and less weathered than surface oil (Short et al. 2004). Polycyclic aromatic hydrocarbons (PAHs) found in benthic invertebrates from oiled areas indicated that lingering oil was still entering the food web (Fukuyama et al. 2000, Carls et al. 2001), where it may have been passed on to higher trophic levels (Meador 1995). The long-term persistence of oil in the environment further supports exposure to residual oil as a source of population-level effects on harlequin ducks.

Exposure to residual oil in organisms at multiple trophic levels of the nearshore community has been indicated by differences in levels of biomarkers of contaminants between oiled and unoiled areas of PWS (Holland-Bartels 2002).

Cytochrome P4501A (CYP1A) is a protein involved in the physiological detoxification and excretion of foreign compounds, including PAHs from petroleum and polychlorinated biphenyls (PCBs; Stegeman et al. 1992). Many nearshore species, including river otters (*Lontra canadensis*), sea otters (*Enhydra lutris*), Barrow's goldeneyes (*Bucephala islandica*), pigeon guillemots (*Cepphus columba*), masked greenling (*Hexagrammus octogrammus*), crescent gunnel (*Pholis laeta*), as well as harlequin ducks, have shown higher CYP1A levels in oiled areas compared to unoiled areas (Duffy et al. 1994, Trust et al. 2000, Holland-Bartels 2002, Jewett et al. 2002). For harlequin ducks, Trust et al. (2000) found induction of CYP1A in birds from oiled sites to be 3 times greater than those from unoiled sites in 1998, and showed that both areas had similar levels of PCBs, supporting the hypothesis that PAHs from petroleum were the cause of increased induction.

Understanding aspects of the winter ecology of harlequin ducks helps shed light on why this species may be especially vulnerable to perturbations such as oil spills on their wintering grounds. Harlequin ducks spend the majority of the annual cycle in rocky intertidal habitats (Robertson and Goudie 1999). As dive-feeders on benthic invertebrate prey, they rely on a community that is a relatively stable source of food; temporal habitat stability favors site fidelity (Johnson and Gaines 1990), and harlequin ducks display a high degree of winter site philopatry, with individuals typically residing along the same stretch of coastline within and among winter seasons (Cooke et al. 2000, Robertson et al. 2000). As a consequence they

are not likely to disperse in the wake of disturbance, and are at higher risk of exposure to lingering oil in contaminated areas of PWS. Additionally, as predators on benthic invertebrates, harlequin ducks may consume PAHs accumulated in prey, and may also physically contact residual oil in the water or sediments while foraging. Having a high mass-specific metabolic rate and relying on a relatively low quality food source, harlequin ducks must maintain very high diurnal foraging rates during winter (Goudie and Ankney 1986, Paulus 1988, Fischer and Griffin 2000), which may lead to high intake of residual oil.

Because behavior is shaped by natural selection to optimize performance within a given environment (Cuthill and Houston 1997), examination of the behavioral effects of contaminants may reveal the connection between contaminant exposure and effects on fitness (Maltby 1999, Weis et al. 2001, Grue 2002). This may be particularly true for species like the harlequin duck, which likely faces high maintenance energy requirements during winter (Goudie and Ankney 1986). Although strong evidence supporting long-term, population-level effects has been found, the link between exposure to residual oil at the level of the individual and population-level effects has not been established for harlequin ducks. Contaminant effects at fine scales (i.e., biochemical, physiological) may alter behavior and reduce performance (Maltby 1999, Weis et al. 2001, Grue et al. 2002). Thus behavioral changes can elucidate the link between contaminant exposure and reduced survival.

The research described here addresses the relationship between harlequin duck behavior and lack of recovery from the *Exxon Valdez* oil spill (EVOS). Chapter 2, "Nocturnal foraging behavior of harlequin ducks wintering in Alaska," investigates the diel foraging patterns of harlequin ducks. Sea ducks (tribe Mergini) as a group have been assumed to forage only during daylight (Owen 1990, McNeil et al. 1992), although recent studies on some species that winter at high latitudes have found evidence of nocturnal foraging (Systad et al. 2000, Systad and Bustnes 2001). Given the high diurnal foraging rates of harlequin ducks and challenging conditions of their northern wintering areas (Goudie and Ankney 1986, Fischer and Griffin 2000), nocturnal foraging may be required to maintain a positive energy budget, particularly during midwinter when day length is short. If harlequin ducks are able to forage at night, reduced photoperiod would not constrain energy intake and nocturnal foraging could compensate for reduced foraging performance and (or) increased energy requirements associated with exposure to oil contamination.

Chapter 3, "Effects of oil ingestion and plumage-oiling on the behavior of harlequin ducks in captivity," describes controlled oil exposure experiments, both with ingested oil and oil applied to plumage, designed to quantify effects of oil exposure on behavior using time-activity budgets. Although physiological effects of exposure to oil contamination have received much attention (reviewed by Leighton 1993), little information exists on the effects of oil contamination on behavior. Behavioral effects of oil exposure may lend insight to how such

exposure may compromise performance in the wild and lead to population-level effects. Controlled experiments with captive harlequin ducks were used to avoid the difficulties inherent in addressing this question in the field, and to allow assessment of dose-response.

Oil spills are conventionally believed to cause severe but relatively short-lived effects on most marine bird populations (Clarke 1984). Evidence from harlequin ducks in the aftermath of the EVOS suggests that this is not always the case, and the work described here is a step toward understanding why, both in terms of the differential vulnerability of species to oil contamination and the effects of oil exposure on behavior. This research also may provide insight into effects of oil contamination beyond PWS and the EVOS. The annual input of petroleum to North American waters averages nearly 110 million liters, 85% of which comes from land-based petroleum consuming activities (NRC 2003). Therefore, it is vital to understand how nearshore predators like the harlequin duck may be affected by chronic, low-level exposure to oil prevalent in many coastal areas.

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CHAPTER 2

NOCTURNAL FORAGING BEHAVIOR OF HARLEQUIN DUCKS
WINTERING IN ALASKA

Daniel J. Rizzolo, Daniel Esler, Daniel D. Roby, and Robert L. Jarvis

Abstract

We monitored radio-tagged harlequin ducks (*Histrionicus histrionicus*) to determine whether nocturnal feeding was part of their foraging strategy in south-central Alaska, near the northern limit of their winter range. Despite attributes of our study site (low ambient temperatures, harsh weather, short day length) and study species (small body size relative to other waterfowl, high daytime foraging rates) that would be expected to favor nocturnal foraging, we found no evidence of nocturnal dive-feeding by radio-tagged harlequin ducks. Radio signals from 8 radio-tagged harlequin ducks detected during an average of 19.5 of 22 nocturnal signal monitoring sessions never exhibited signal loss due to diving during a total of 780 minutes of signal monitoring. In contrast, the same 8 radio-tagged birds were detected during an average of 9.1 of 12 daytime monitoring sessions and signal loss indicating diving occurred during $62 \pm 7\%$ of 5-minute daytime monitoring periods (a total of 364 minutes of signal monitoring). Our results suggest that nocturnal foraging is not an adaptive strategy for harlequin ducks, possibly due to reduced foraging efficiency and (or) increased predation risk at night. Given the time constraint on diurnal foraging during midwinter at high latitudes and the apparent absence of nocturnal feeding in their behavioral repertoire, harlequin ducks may be particularly sensitive to disturbance and other factors that reduce diurnal foraging efficiency or increase energy requirements on the wintering grounds.

Introduction

Foraging behavior can be adjusted in response to changing conditions to optimize energy intake (Schoener 1971, Pyke 1977). Thus foraging behavior is fundamentally linked to fitness because energy intake has direct effects on survival. Birds have been shown to increase their foraging activity in association with increased maintenance energy costs and (or) decreased food availability (Owen et al. 1992, Percival and Evans 1997, McKnight 1998, Webster and Weathers 2000, Cope 2003). Some species that normally feed only during daylight extend foraging into the nocturnal period in response to reduced day length, or disturbance during diurnal foraging time (Thornburg 1973, Lane and Hassel 1996, Systad et al. 2000, Systad and Bustness 2001). Sea ducks (tribe Mergini) are generally believed to be visual foragers limited by light conditions to diurnal foraging (Owen 1990, McNeil et al. 1992), although few data exist to support this assumption (Guillemette 1998). However, recent studies of sea ducks wintering at high latitudes have found that some species feed during darkness when day length is short (Systad et al. 2000, Systad and Bustnes 2001).

Requirements for energetically efficient foraging in harlequin ducks (*Histrionicus histrionicus*) are likely highest during mid-winter when harsh environmental conditions increase maintenance energy requirements, while short day length decreases the time available for diurnal foraging (Goudie and Ankney 1986). Among sea ducks, harlequin ducks are small-bodied (0.4-0.8 kg), and hence have higher mass-specific metabolic rates and are less able to rely on stored

reserves for extended periods (Calder 1974). This may be particularly true during periods of cold stress due to high thermostatic costs. Indeed, foraging accounts for > 70% of harlequin duck diurnal activity in the winter, and time spent foraging has been found to be negatively correlated with temperature and day length (Goudie and Ankney 1986, Fischer and Griffin 2000). Given the high proportion of the day spent feeding, harlequin ducks face stringent time constraints on increasing diurnal foraging time (Goudie and Ankney 1986). Nocturnal foraging, however, could ease the constraint of short day length for harlequin ducks wintering at high latitudes.

We examined the nocturnal behavior of harlequin ducks wintering in Resurrection Bay, on the south-central coast of Alaska, near the northern limit of their winter range (Robertson and Goudie 1999). Using radio telemetry, we looked for evidence of dive-feeding at night during the winter of 2001-02. Our objective was to better understand the winter foraging ecology of harlequin ducks and to directly test the assumption that sea ducks are constrained to forage during daylight. Also, harlequin ducks are considered to be particularly sensitive to changes in their wintering environment and have been shown to respond more strongly than other species to anthropogenic disturbance (Esler et al. 2002). Therefore, the results of this study are relevant for evaluating whether harlequin ducks can employ nocturnal foraging to accommodate anthropogenic disturbance and other factors limiting foraging efficiency on the wintering grounds.

Methods

This study was conducted in Resurrection Bay (60.1° N, 149.4°W), a glacial fjord located on the southeast side of the Kenai Peninsula, Alaska, USA. Harlequin ducks were captured at Lowell Point, an alluvial fan on the west side of the bay ca. 3 km south of the town of Seward. The shoreline immediately north and south of Lowell Point is steeply sloped, dropping immediately into subtidal habitat, while the point is gently sloping with a large expanse of intertidal habitat composed of boulder, cobble, and gravel sediment. Maximum tide range is 5 m and strong north-south winds are typical during winter months. A group of ca. 35 harlequin ducks wintered along Lowell Point in 2001-02.

On 13 and 14 October 2001 we captured harlequin ducks using a modified floating mist net (Kaiser et al. 1995). Ten harlequin ducks, 6 males and 4 females, were captured and surgically implanted with radio transmitters (HoloHill Systems Ltd., Ontario, Canada). Radio-transmitters were 18.8 g (< 3% of adult body mass), with a 6-month battery life expectancy, a pulse rate of 44-46 pulses per minute, and a mortality switch that doubled the pulse rate if the transmitter remained motionless for ≥ 12 h. Surgeries to implant radio-transmitters were conducted at the Alaska SeaLife Center in Seward by a veterinarian experienced with the procedure and under protocols approved by the Institutional Animal Care and Use Committee of the Alaska SeaLife Center (protocol 00-005). Surgically implanted transmitters have been used successfully in previous studies with harlequin ducks and were

found to carry a low risk of mortality (Mulcahy and Esler 1999). Radio-tagged birds were held for one hour after surgery and then released at the capture location.

Radio signals were monitored from a remote telemetry station consisting of 2 mast-mounted, 4-element Yagi antennae connected to an Advanced Telemetry System R4000 receiver (Isanti, Minnesota, USA) located on the hillside above the capture location at an elevation of ca. 70 m. Loss of radio-signal reception was used as an indicator of diving behavior (Custer et al. 1996, Jodice and Collopy 1999). Daytime visual observations of radio-tagged birds confirmed that pulses were inaudible during dives and audible again upon resurfacing. During each radio signal monitoring session, the radio frequency from each radio-tagged bird was monitored for signal reception loss caused by diving behavior during a period of 5 minutes. Radio-tagged birds not detected were recorded as absent from the study area. Radio signals were monitored at least once per week from November 2001 through March 2002.

Detection rates during diurnal and nocturnal signal monitoring sessions were calculated for each radio-tagged bird as the percentage of signal monitoring sessions during which each bird was present in the study area. Diurnal and nocturnal detection rates were averaged across all radio-tagged birds. For each radio-tagged bird, the percentage of 5-minute signal monitoring sessions during which the bird was present in the study area and diving occurred was calculated and averaged across all birds for either diurnal or nocturnal periods as an estimate of diving frequency. All estimates are presented as the mean \pm 1 standard error.

Results

Of the 10 harlequin ducks radio-tagged, one was never detected after release and we assume that the bird left the study area, or the radio failed immediately.

The radio signal from a second radio-tagged bird was not heard until 7 weeks after release when its mortality signal was detected and the freshly-killed carcass was found in a tree commonly used by bald eagles (*Haliaeetus leucocephalus*).

Because these 2 birds were never detected in the study area alive, they did not contribute signal monitoring data. The remaining 8 radio-tagged birds stayed within the study area for the duration of the study.

Signals from radio-tagged harlequin ducks were monitored during a total of 34 sessions between November 2001 and March 2002: 22 at night and 12 during the day. Signal monitoring sessions were distributed throughout both the diurnal and nocturnal periods and were conducted across a broad range of tide heights and weather conditions. Most radio-tagged birds were detected during each signal monitoring session, although the average number of birds detected during nocturnal sessions (7.0 ± 0.2) was slightly greater than the average number detected during diurnal sessions (6.2 ± 0.3). The average detection rate of each radio-tagged bird during nocturnal signal monitoring session was $89 \pm 2\%$ (an average of 19.5 out of 22 nocturnal sessions) and was less variable than the average detection rate during diurnal signal monitoring sessions ($76 \pm 10\%$, or an average of 9.1 out of 12 diurnal occasions; Table 2.1). Signal loss indicative of diving was not heard in the signal

Table 2.1. Diurnal and nocturnal detections of 8 radio-tagged harlequin ducks in Resurrection Bay, Alaska during winter 2001-02. The signal of each radio-tagged bird was monitored for one 5-minute period for presence in the study area and signal loss indicative of diving behavior during 12 diurnal and 22 nocturnal monitoring sessions.

Radio Frequency	Diurnal period		Nocturnal period	
	Number of detections (n = 12)	Number of detections with diving	Number of detections (n = 22)	Number of detections with diving
6.903	3	1	17	0
7.032	8	6	20	0
7.056	12	9	20	0
7.207	12	9	21	0
7.221	12	9	18	0
7.245	3	1	19	0
7.307	12	7	20	0
7.320	11	8	21	0
Average \pm SE	9.1 \pm 1.4	6.2 \pm 1.2	19.5 \pm 0.5	0.0 \pm 0.0

of any radio-tagged harlequin duck detected during a total of 780 minutes of nocturnal monitoring. In contrast, signal loss indicative of diving was heard during an average $62 \pm 7\%$ of diurnal detections of birds present in the study area (a total of 364 minutes of signal monitoring; Table 2.1). Thus diving behavior was never detected at night, but was detected frequently during the day.

Discussion

We found no evidence that radio-tagged harlequin ducks wintering in Resurrection Bay during our study period foraged by diving at night. High nocturnal detection rates and absence of signal loss indicative of diving behavior support the hypothesis that harlequin ducks rest in groups offshore at night (Fischer and Griffin 2000, Rodway and Cooke 2001). The lower and more variable average detection rate during the day compared to at night, and the high percentage of daytime detections with signal loss due to diving may reflect higher levels of activity and movements to feeding areas out of detection range.

Conditions in Resurrection Bay during the study period were likely energetically demanding for harlequin ducks. Average daily temperature was -4.4 °C (range -23.9 to 6.1 °C; NOAA 2002), while average photoperiod length, including crepuscular periods, was 8.3 hours (range 6.8 to 11.4 hours; U. S. Navy 2002). Average temperature during signal monitoring sessions conducted on the shortest days in December, when diurnal feeding time was most constrained, was

-3.5 °C. Despite these conditions, the radio-tagged harlequin ducks in this study apparently fed very little, if at all, by diving at night.

The apparent absence of nocturnal dive-feeding behavior in harlequin ducks may indicate that dive-feeding is not energetically profitable at night. Nilsson (1970) speculated that sessile prey items may be more available to dive-feeding waterfowl at night than motile prey. Sessile prey compose only a portion of the winter diet of harlequin ducks (Vermeer 1983, Gains and Fitzner 1987, Goudie and Ankney 1986, Fischer and Griffin 2000). If motile prey are unavailable at night, the overall density of available prey for nocturnally foraging birds would be reduced relative to prey densities encountered during the day. In addition, the sessile prey in the diet of wintering harlequin ducks have lower energy content than motile prey (Goudie and Ankney 1986, Fischer and Griffin 2000). Given that diving is an energetically expensive behavior (Lovvorn and Jones 1991), and capture success would likely be reduced by decreased prey density and decreased prey conspicuousness at night (Schoener 1971), nocturnal dive-feeding may carry a high risk of incurring a negative energy balance.

Systad and Bustnes (2001) found that Steller's eiders (*Polysticta stelleri*) wintering at 70°N in Norway foraged at night. Increased use of non-diving foraging behaviors (surface-feeding, up-ending) and increased foraging activity during low tide by Steller's eiders likely reduced foraging costs (Systad and Bustnes 2001). The winter diet of Steller's eiders is similar to that of harlequin ducks, composed of both sessile and motile benthic invertebrates (Bustnes et al.

2000), and the Steller's eider is known to feed in dense kelp beds that contain a high density of invertebrate prey (Bustnes and Systad 2001). Harlequin ducks in winter are associated with nearshore rocky habitats (Goudie and Ankney 1988, Esler et al. 2000a), and are not as strongly associated with dense vegetation as Steller's eiders (Bustnes and Systad 2001). Differences in the density of prey in preferred feeding habitats may explain the difference in foraging strategies during winter between harlequin ducks and Steller's eiders.

Harlequin ducks wintering at Lowell Point were observed to feed using non-diving behaviors during the day; however, non-dive feeding was always observed in association with dive-feeding. Fischer and Griffin found that harlequin ducks wintering in the Aleutian Islands in Alaska fed more during high tides, when, presumably, foraging by non-diving behaviors would be most restricted.

Additionally, harlequin ducks at Lowell Point were observed to move offshore shortly after sunset, as has been documented in other wintering areas (Fischer and Griffin 2000, Rodway and Cooke 2001). On several occasions, the shoreline of Lowell Point was searched for radio-tagged birds following nocturnal signal monitoring sessions using a hand-held antenna and receiver, and no birds were located nearshore based on low signal strength.

Rodway and Cooke (2001) postulated that evening departures from the nearshore by harlequin ducks may indicate a response to increased predation risk from nocturnally active predators (e.g., mink *Mustela vison*). We speculate that the apparent absence of nocturnal foraging in harlequin ducks during winter may be

related to low prey densities available at night in rocky, nearshore habitats and (or) high nighttime predation risk, both of which may make nocturnal feeding unprofitable.

The most adaptive strategy for harlequin ducks wintering in Resurrection Bay may be to forego dive-feeding at night until favorable foraging conditions return with daylight. Foraging is profitable when the rate of energy assimilation exceeds the rate of energy expenditure, which for dive-feeding waterfowl is primarily related to overcoming the cost of buoyancy during descent (Lovvorn and Jones 1991). Wintering American black ducks (*Anas rubripes*) that foraged only during daylight by diving for low quality aquatic vegetation decreased feeding during periods of low ambient temperatures, suggesting that dive-feeding was no longer profitable when thermostatic costs were high (Brodsky and Weatherhead 1985). However, king eiders (*Somateria spectabilis*) and common eiders (*S. mollissima*), both large species of sea ducks that feed on sessile invertebrates by diving, responded to the reduced photoperiod and harsh weather conditions of their 70° N latitude wintering site by foraging in afternoon darkness (Systad et al. 2000). This suggests that diving ducks may forage nocturnally when prey densities are sufficiently high and foraging costs are sufficiently low to make nocturnal foraging more profitable than relying on stored reserves to meet maintenance energy requirements.

Harlequin ducks in winter maintain very high diurnal foraging rates to meet daily energy requirements and may minimize energy expenditure at night by

resting, when foraging conditions are likely poor. This hypothesis is supported by increased foraging rates during the evening by harlequin ducks in winter which suggest preparation for a period of non-feeding during the night (Goudie and Ankney 1986, Fischer and Griffin 2000, Heath et al. in press). The apparent absence of nocturnal dive-feeding found in the present study, in addition to offshore movements at night, suggest that harlequin ducks do not feed at night during winter. Reduced day length during mid-winter on northern wintering grounds, therefore, places stringent constraints on the amount of time available for diurnal foraging by harlequin ducks.

Esler et al. (2000b) found that harlequin duck survival was reduced in areas affected by the *Exxon Valdez* oil spill compared to unoiled areas, and speculated that subtle changes in energy and (or) time-activity budgets as a result of continued exposure to oil may have caused the observed differences in survival. Our finding that harlequin ducks rarely, if ever, feed at night and thus would be unable to use nocturnal foraging to compensate for the effects of disturbance is consistent with this hypothesis, and extends to other forms of anthropogenic alterations of wintering habitat for harlequin ducks.

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CHAPTER 3

EFFECTS OF CRUDE OIL INGESTION AND PLUMAGE-OILING ON
BEHAVIOR OF HARLEQUIN DUCKS IN CAPTIVITY

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Abstract

Harlequin ducks (*Histrionicus histrionicus*) in Prince William Sound (PWS), Alaska, USA have shown evidence of long-term effects from the 1989 *Exxon Valdez* oil spill as many as 9 years after the spill. We conducted oil-dosing and plumage-oiling experiments using adult female harlequin ducks in captivity to test the hypothesis that the effects of exposure to weathered Prudhoe Bay crude oil on the time-activity budgets of harlequin ducks may have contributed to the lower survival observed in oiled areas of PWS. We found no effect of ingestion of crude oil on the occurrence of feeding activity during 30-minute observation periods, or on time spent feeding. Effects of crude oil ingestion on maintenance activity were detected, but were neither consistent between the 2 years of the study, nor dose-dependent for the 2 doses administered (2 and 20 mL kg⁻¹ wk⁻¹), and therefore did not strongly support an oil-dosing effect on maintenance activity. Consequently, our results did not support the hypothesis that oil ingestion affects time-activity budgets of captive harlequin ducks, at least for the doses and conditions of captivity used in this study. In contrast, plumage-oiling reduced feeding activity in captive harlequin ducks. The estimated probability of feeding during 30-minute observation periods for birds in the high-exposure treatment (5 mL of crude oil) was 53% less than that of non-oiled controls. Oiled birds exhibited reduced time spent feeding with increased level of external-oiling; this effect was greatest among birds in the high-exposure treatment, which spent 43% less time feeding than non-

oiled birds. Reduced feeding was associated with less time in the water diving and presumably lower heat loss. Trends in both the occurrence of maintenance activity and time spent in maintenance activity by birds in the high-exposure treatment were suggestive but inconclusive that plumage-oiling increased maintenance activity. The behavioral changes associated with plumage-oiling in captivity may reduce fitness in the wild where a high proportion of time must be spent in the water feeding. Our results are consistent with the hypothesis that plumage-oiling could contribute to the observed lower survival of adult female harlequin ducks wintering in oiled areas of PWS. The occurrence and extent of external exposure to residual oil in harlequin ducks wintering in oiled areas, however, has not been measured.

Introduction

Harlequin ducks (*Histrionicus histrionicus*) wintering in areas of Prince William Sound, Alaska (PWS) that were oiled following the 1989 *Exxon Valdez* oil spill (EVOS) continued to exhibit oil spill effects as many as 9 years after the spill (Esler et al. 2002). Effects on harlequin ducks wintering in oiled areas of PWS included lower than expected densities (Esler et al. 2000a), numerical declines (Rosenberg and Petrula 1998), reduced winter survival (Esler et al. 2000b), and elevated levels of the biomarker cytochrome P4501A (CYP1A) attributed to exposure to residual oil (Trust et al. 2000). These findings provide strong evidence

of oil spill effects beyond the short-term, acute effects conventionally thought to be most damaging to avian populations (Esler et al. 2002). It is poorly understood, however, how chronic, low-level exposure to residual oil may compromise survival and affect harlequin duck populations. In this study we examined the effects of chronic oil exposure, both internal and external, on behavior of harlequin ducks as a possible mechanism contributing to lower winter survival observed in oiled areas of PWS.

Harlequin ducks occupy rocky, nearshore marine habitats during the nonbreeding season and show strong fidelity to coastal wintering sites (Robertson and Goudie 1999, Cooke et al. 2000, Robertson et al. 2000). Forty percent of the nearly 42 million liters of Prudhoe Bay crude oil released into PWS during the EVOS was deposited in biologically productive intertidal and shallow subtidal habitats (Galt et al. 1991, Wolfe et al. 1994). Residual oil has persisted in the environment through at least 2001 (Short et al. 2004), as has the potential for chronic exposure and long-term effects from the oil spill. Several nearshore mammal and bird species, including river otters (*Lontra canadensis*), sea otters (*Enhydra lutris*), and pigeon guillemots (*Cephus columba*), have shown evidence of long-term effects from the EVOS, providing further support for a link between dependence on the nearshore environment and chronic effects of oil contamination (Bodkin et al. 2002, Golet et al. 2002, Bowyer et al. 2003).

Harlequin ducks in PWS may encounter residual oil through 2 routes: (1) indirectly by ingesting contaminated prey; and (2) directly by contacting oil in the water column or in sediments and subsequently ingesting oil while preening contaminated feathers. The diet of harlequin ducks in winter is largely composed of benthic invertebrates, which accumulate polycyclic aromatic hydrocarbons (PAHs) from residual oil in their tissues, and, potentially, may transfer these contaminants to higher trophic levels (Meador et al. 1995). Oil contamination was documented in benthic invertebrates from the EVOS zone through at least 1995 (Fukuyama 2000, Carls et al. 2001), implicating ingestion as a likely source of exposure. External exposure may occur if residual oil trapped in sediment is returned to the water column during storms or through excavation by foraging animals such as sea otters (Bodkin et al. 2002). Although long-term plumage-oiling has not been investigated in harlequin ducks, traces of hydrocarbons were found on the pelage of river otters from oiled areas 8 years after the oil spill (Duffy et al. 1999). Plumage-oiling may also lead to ingestion of oil while preening feathers after they become contaminated with oil (Hartung 1963). Therefore, the risk of chronic exposure to residual oil exists for the highly philopatric, nearshore-dependent harlequin duck.

Laboratory studies have found that captive mallard ducks (*Anas platyrhynchos*) tolerate ingestion of surprisingly large amounts of crude oil without obvious negative effects (Coon and Dieter 1981, Rattner 1981, Stubblefield et al.

1995, Boehm et al. 1996). These results have been used to infer similar tolerance in harlequin ducks in PWS (Stubblefield et al. 1995, Boehm et al. 1996). However, oil ingestion in combination with environmental stressors, such as low ambient temperatures, have been shown to cause increased mortality in waterfowl (Holmes et al. 1978, 1979). Environmental conditions, therefore, may play an important role in how animals respond to exposure to contaminants (Gordon 2003); such environment-dependent effects might be missed under more benign laboratory conditions.

While a number of studies have addressed the biochemical and physiological effects of oil ingestion (reviewed by Leighton 1993), few have looked at how these effects might translate into changes in behavior. Increased food consumption was documented in oil-dosed mallard ducks (Holmes et al. 1978, 1979) and American kestrels (*Falco sparverius*; Pattee and Franson 1982), suggesting a corresponding increase in feeding activity. Sandhill cranes (*Grus americanus*) became lethargic after oil-dosing (Fleming et al. 1982), and oil-dosed mallard ducklings exhibited reduced avoidance behavior (Szaro et al. 1978). Additionally, the effects of oil ingestion vary among species (Leighton 1993), and no previous studies of the toxicological effects of oil ingestion on harlequin ducks have been conducted.

The most conspicuous effects of oil contamination on birds are those related to oiling of the plumage, which causes loss of the water repellent and insulative

qualities of feathers and a consequent increase in the metabolic cost of thermoregulation (Hartung 1967, Leighton 1993, Jenssen 1994). This increase in thermoregulatory costs may lead to changes in behavior, such as increased feeding to boost energy intake, and increased maintenance behaviors to remove oil and restore water repellency. External-oiling has been associated with: (1) an increase in maintenance behaviors and reduced time spent in the water for common eiders (*Somateria mollissima*) under semi-natural conditions (Ekker et al. 1989); (2) increased maintenance behavior, reduced resting, and increased aggressive interactions in captive sanderlings (*Calidris alba*; Burger and Tsipoura 1998); and (3) increased maintenance and reduced feeding in free-ranging sanderlings and semipalmated plovers (*Charadrius semipalmatus*; Burger 1997).

Changes in behavior related to oil ingestion or external-oiling, singly or in combination, may contribute to reduced survival in harlequin ducks wintering in PWS. South-central Alaska is near the northern limit of the winter range for harlequin ducks, and winter conditions may make it the most challenging period of their annual cycle (Goudie and Ankney 1986). Among sea ducks (tribe Mergini), harlequin ducks are small-bodied and, consequently, have a high mass-specific metabolic rate, high surface area to volume ratio, and limited ability to rely on stored reserves to meet increased energetic demands (Calder 1974). Feeding activity dominates their time-activity budget during winter, accounting for > 70% of daylight hours (Goudie and Ankney 1986, Fischer and Griffin 2000). In addition to

maintaining a high foraging effort during winter, sea ducks rely on highly insulative plumage to reduce the metabolic costs of thermoregulation (Jenssen and Ekker 1989, Jenssen et al. 1989). Thus, foraging efficiency, as well as maintenance of plumage quality, are likely critical to the winter survival of harlequin ducks. Any changes in these components of the time-activity budget of harlequin ducks related to oil exposure would presumably reduce survival during the winter.

Determining effects of oil exposure on behavior using free-ranging harlequin ducks in PWS would be difficult due to inter-individual variation in exposure to residual oil and differences in the degree of oil contamination among local wintering sites. In the experiments described here, we used controlled levels of oil ingestion and plumage-oiling in wild-caught, adult female harlequin ducks maintained under natural climate and photoperiod conditions at 60°N latitude to investigate changes in time-activity budgets caused by oil exposure. We used an information theoretic approach (Burnham and Anderson 2002) to select the model(s) that best account for variation in the behavior of captive harlequin ducks. We predicted that if oil exposure altered behavior, analysis results would strongly support oil exposure treatment as an important variable for explaining variation in the behavioral responses of interest, and estimated response values would differ for oil-exposed and control treatment groups.

Methods

Capture and Captive Husbandry

We captured 25 adult female harlequin ducks during wing molt from the northwest coast of Montague Island (60.2°N, 147.2°W), Prince William Sound, Alaska, USA during early September in each of 2 years (2000 and 2001). The capture location was not oiled during the EVOS (Galt et al. 1991, Wolfe et al. 1994). Harlequin ducks are highly philopatric to wintering sites (Cooke et al. 2000, Robertson et al. 2000), so captured birds were likely to have lived consistently in the unoiled area. Flightless birds were herded with sea kayaks into a corral trap placed along the shoreline. Captured birds were sexed by plumage characteristics and cloacal anatomy, and age-class (hatch-year, after-second-year) was determined by bursal depth (Mather and Esler 1999). Adult (after-second-year) female harlequin ducks captured in each year were transported by float plane from the capture site to the Alaska SeaLife Center (ASLC) in Seward, Alaska (60.1°N, 149.4°W), where they were held in captivity for the duration of the winter and used as subjects in the experiments described below. The focus of this work was on adult females because female survival has a strong influence on the population dynamics of long-lived species like harlequin ducks (Schmutz et al. 1997).

Captive harlequin ducks were housed in a mesh-enclosed outdoor pen exposed to local climate and photoperiod conditions. The enclosure was partitioned into three 3.7 × 3.7 m sections, each with a flowing seawater pool

(2000-01: diameter 1.8 m, depth 0.9 m; 2001-02: diameter 2.4 m, depth 0.6 m). Birds were fed an *ad libitum* diet of commercially obtained Atlantic silversides (*Menidia menidia*) presented in trays on land during winter 2000-01, and an *ad libitum* mixed diet of Atlantic silversides and Antarctic krill (*Euphausia superba*) placed in the pools during winter 2001-02. The changes in diet composition and presentation made in the second year of the study were intended to increase foraging effort, which was low under the conditions of the first year of the study.

Oil Ingestion Experiments

In both years of the oil ingestion experiment, birds were given 4 weeks to acclimate to the captive environment and diet before the start of oil-dosing. After acclimation, the 21 birds that had adjusted to captivity best, based on maintenance of body mass, were randomly assigned to 1 of 3 treatments (control, low-dose, high-dose), each with 7 birds. The birds assigned to each treatment group were kept together in one of the 3 partitions of the outdoor enclosure to avoid potential cross-contamination between oil-dosed and control individuals; however, each of the 3 sections of the enclosure were identical and thus were not expected to differentially affect the behavior of the birds housed in them. Each bird was banded with a pair of colored plastic tarsus bands to allow identification of individuals. The average body mass (± 1 SD) of the female harlequin ducks used in the study was 523.6 ± 27.2 g and was similar in both years.

Different dosing regimes were used in the 2 years of the oil ingestion experiment (Table 3.1). In 2000, dosing was conducted twice weekly. Low-dose birds were fed 1 mL of oil per kg body mass at each dosing, high-dose birds were fed 10 mL of oil per kg body mass at each dosing, and controls were fed no oil, although they were handled identically to the dosed birds. Doses were administered orally via gavage with a syringe and feeding tube; control birds were gavaged with an empty feeding tube. Dosing was done in the morning before birds had fed.

We changed the dosing regime in the second year of the study to better simulate low-level, intermittent ingestion of weathered crude oil. During winter 2001-02, dosing was conducted every other day in the evening, after birds had fed. Low-dose birds were fed 0.57 mL of oil per kg body mass at each dosing, high-dose birds were fed 5.71 mL of oil per kg body mass at each dosing, and control birds were handled identically, but were fed no oil. The average cumulative dose per week for each treatment was equivalent in both years of the study (low-dose 2 mL kg⁻¹ wk⁻¹, high-dose 20 mL kg⁻¹ wk⁻¹), but doses were smaller and more frequent in the second year. In both years, birds were held for 60-90 minutes after dosing in an indoor, mesh-bottomed pen before being returned to the outdoor enclosure to prevent contamination of pools and subsequent plumage-oiling by oily excreta.

We dosed birds with weathered crude oil from Prudhoe Bay, Alaska. To simulate weathering, crude oil was mixed with seawater and stirred continuously for 10 days at 25°C, after which it was separated from water and stored in air tight

Table 3.1. Oil-dosing regimes administered to captive harlequin ducks in each of two winters of oil-dosing experiments at the Alaska SeaLife Center, Seward, Alaska.

Year	Oil-dosing treatment	n	Crude oil dose (mL kg ⁻¹)	Dosing frequency	Average cumulative dose (mL kg ⁻¹ wk ⁻¹)
2000-01	Control	7	0.00	Twice weekly	0.0
	Low-dose	7	1.00	Twice weekly	2.0
	High-dose	7	10.00	Twice weekly	20.0
2001-02	Control	7	0.00	Every other day	0.0
	Low-dose	7	0.57	Every other day	2.0
	High-dose	7	5.71	Every other day	20.0

containers until dosing (Ben-David et al. 1999). Doses were based on body masses measured at the previous handling event. Dosing occurred between 15 October 2000 and 20 February 2001 during the first year of the study (total dosings = 37), and between 15 October 2001 and 10 February 2002 in the second year of the study (total dosings = 60). Birds that became sick during the course of the experiment were treated by ASLC veterinary staff. If possible, oil-dosing was continued through the course of treatment; however, no data were collected until sick birds returned to good health, as judged by the veterinary staff. If the illness was severe, the sick bird was removed permanently from the experiment for treatment. Mortalities unrelated to oil-dosing occurred during both winters of the experiment leading to a final sample size of 17 subjects in each year.

Behavioral observations

Time-activity budgets were quantified by following a focal individual continuously and recording the duration of time spent in each category of activity during a 30-minute observation period (Altmann 1974). Activities were categorized as either feeding, maintenance (preening, bathing, stretching, comfort movements), locomotion (walking, swimming, flying), resting (sleeping, loafing), social (agonistic interactions), or drinking. Feeding activity in winter 2000-01, when birds fed from trays, consisted of handling food items; in winter 2001-02, when feeding required diving for food, feeding activity consisted of time spent

searching, diving, and handling food items. Time spent in activities was recorded using *The Observer* software (Noldus Information and Technology 1991) and a notebook computer. One observer (DJR) conducted all behavioral observations using binoculars from an elevated blind located 10 m from the outdoor enclosure.

Birds were observed in a random sequence; no resampling occurred until all birds had been sampled in the prior round of observations. Start times were randomly determined within 3 equal diurnal periods (morning, afternoon, evening) beginning 30 minutes prior to sunrise and continuing until 30 minutes after sunset. On each sampling day, 1 bird from each treatment was sampled during each of the 3 diurnal periods, for a total of 9 observations on each sampling day. Temperature (°C), estimated wind speed (Beaufort scale), and day length (minutes) were recorded at the start of each observation session.

During the second year of the study, the feeding protocol was modified several times during the first 6 weeks of dosing; therefore, only behavioral observations conducted after these modifications were complete (6 December 2001) were included in analyses. Three birds died from causes unrelated to oil-dosing between the start of dosing in winter 2001-02 and the start of behavioral observations; consequently, time-activity budget data used for analyses were collected from only 18 birds during winter 2001-02.

Plumage-oiling Experiment

We conducted a plumage-oiling experiment between 21 February and 18 March 2002, drawing subjects from the group of birds used in the oil ingestion experiment conducted earlier that winter. Ten days after the conclusion of the oil ingestion experiment, we randomly assigned 16 birds to 3 plumage-oiling treatments. Plumage-oiling treatments consisted of a lightly-oiled group exposed to 1 mL of crude oil for 40 minutes ($n = 6$ birds), a moderately-oiled group exposed to 2.5 mL of crude oil for 50 minutes ($n = 4$ birds), and a heavily-oiled group exposed to 5.0 mL of oil for 60 minutes ($n = 6$ birds). Birds were individually exposed to weathered Prudhoe Bay crude oil in the laboratory while at rest in a tub containing 14 L of seawater. After a 10-minute acclimation period, weathered crude oil was injected into the tub through a port using a syringe. The experiment was conducted over three 1-week periods. Birds from 2 treatments were oiled on day 1 of each week-long oiling period and remained oiled for the entirety of the 7-day period.

After oil exposure, birds were housed in the outdoor enclosure described previously. Behavioral observations were conducted over each 7-day experimental period using the same protocol used during the oil ingestion experiment. The behavior of 1 to 4 randomly selected, non-oiled birds was sampled during each observation session during the first 2 weeks of the experiment as controls. Birds that had been oiled and washed during a previous week of the experiment were not included in the pool of control birds; by the final week of the experiment no birds

remained that had not been previously oiled (i.e., no control observations were conducted during the final week).

All methods and procedures were approved by the Institutional Animal Care and Use Committee of the Alaska SeaLife Center under protocols 000-004 and 02-002.

Data Analysis

We focused our analyses on the 2 activities most likely to influence the winter survival of harlequin ducks: feeding and maintenance. Harlequin ducks may adjust time-activity budgets at multiple scales, including the frequency of occurrence of each activity, as well as duration of time spent in each activity. Because feeding and maintenance activities did not occur during all 30-minute observation periods, we analyzed the data in 2 stages: (1) the presence or absence of an activity during an observation period was treated as a binary response and analyzed using logistic regression models; and (2) for the subset of observation periods during which the activity of interest occurred, the proportion of time spent in the activity was analyzed using general linear mixed models. This analytical approach addressed both the factors affecting the probability that the activity would occur during a given 30-minute observation period, and the factors affecting the time spent in the activity when it was observed.

We used an information theoretic approach (Akaike Information Criterion, AIC; Burnham and Anderson 2002) to select the best-fitting model(s) from among a set of *a priori* candidate models. AIC evaluates the strength of evidence for each model using the principle of parsimony to balance model fit (log likelihood) with model complexity (number of parameters). The model having the lowest AIC value was interpreted as being best supported by the data from among the models considered. We used AIC adjusted for small sample sizes (AIC_c) for all data other than binary responses exhibiting overdispersion, for which we used $QAIC_c$, the quasi-likelihood adjustment of AIC_c (Burnham and Anderson 2002). Models in a given candidate set were ranked according to their AIC values, and the difference between the top-ranked model and each subsequent model, ΔAIC , was calculated. Models with $\Delta AIC \leq 2$ were considered to be strongly supported by the data (Burnham and Anderson 2002).

We calculated Akaike weights to evaluate the strength of evidence for each model and to estimate model-selection uncertainty. Akaike weights within a set of candidate models are standardized to sum to 1, and, therefore, an Akaike model weight near 1.0 indicates a high probability of being the best model given repeated samples (Burnham and Anderson 2002). Model-selection uncertainty was incorporated into parameter estimates and measures of precision using model averaging based on Akaike weights (eqs. 4.1 and 4.6, respectively; Burnham and Anderson 2002). Model-averaged estimates are less biased than estimates from a

single, top-ranked model when the top-ranked model is not strongly supported (i.e., an Akaike model weight < 0.90). The relative support for each explanatory variable included in a candidate model set was evaluated by summing the Akaike weights from all models that included each explanatory variable (Burnham and Anderson 2002). Thus, explanatory variables that occur in most or all of the models most supported by the data will have high summed Akaike weights (close to 1.0), and are therefore well-supported for drawing inferences (Burnham and Anderson 2002).

Time-activity budgets of wintering waterfowl are known to vary with a number of time and weather variables (Brodsky and Weatherhead 1985, Goudie and Ankney 1986, Fischer and Griffin 2000). However, the behavioral response to these variables may differ under the conditions of captivity. Therefore, the sets of candidate models we evaluated were necessarily broad. None of the explanatory variables considered in any model set were highly correlated, and all models were judged to be biologically plausible prior to inclusion in the candidate set. Because candidate model sets were large, we based our inference primarily on the relative support for explanatory variables across models (summed Akaike weights for explanatory variables) and unconditional 95% confidence interval coverage around model-averaged, adjusted mean estimates of response variables for each oil treatment group, rather than basing inference on a particular model or set of models.

Explanatory variables considered for the oil-dosing experiment included: oil-dosing treatment (TREAT: control, low-dose, high-dose; categorical), time of

day (DIURN: morning, afternoon, evening; categorical), wind speed (WIND: low 0-6 knots, moderate 7-21 knots, high 22⁺ knots; categorical), temperature (temp: °C; continuous), day length (dayl: minutes of photoperiod; continuous), and year (YEAR: winter 2000-01, winter 2001-02; categorical). Categorical variables were included as indicator variables, with the first level of each designated as a reference level (Ramsey and Schafer 2002). Models including interactions always included the main effects of interactive terms (Ramsey and Schafer 2002).

Candidate models, both logistic regression and general linear mixed, considered in the analysis of feeding and maintenance activities by oil-dosed harlequin ducks consisted of all possible combinations of main effects of the explanatory variables temp, dayl, DIURN, TREAT, YEAR, and the TREAT × YEAR interaction, as well as an intercept-only null model, for a total of 41 candidate models (Appendix A). The effects of oil ingestion on behavior were considered *a priori* to be physiologically based and additive to the extrinsic effects of the environment (Holmes et al. 1978, 1979). We constrained all models to include YEAR to account for expected changes in behavior related to differences in feeding protocol between years. The TREAT × YEAR interaction was considered to account for the potential influence of differences in feeding protocol and (or) dosing regime on the behavioral response to oil-dosing. Changes in response with time were confounded with changes in day length through the season, and therefore only day length was included as an explanatory variable in the models.

Behavior of externally-oiled birds was evaluated in relation to the same set of explanatory variables as considered for the oil-dosing experiment; however, because day length did not vary substantially over the 7-day experimental periods, it was not included. The effect of external-oiling on feeding activity was expected to operate through increased thermoregulatory costs, which could vary with temperature and wind speed. Interactions between external-oiling treatment and weather variables (TREAT \times temp, TREAT \times WIND) were included in the set of logistic regression models for the probability of feeding. For these data, wind speed was included as a 2-level categorical variable (WIND: low 0-6 knots, moderate-high 7⁺ knots) to allow evaluation of the TREAT \times WIND interaction with the limited data available (i.e., not all oiling treatments were observed under the original wind speed categories). Time of day was included as a 2-level categorical variable because observations were made only during afternoon and evening periods. Linear and quadratic trends in feeding as a function of days post-oiling (day; continuous) were considered as interactions with TREAT to allow estimation of a separate slope parameter for each treatment (TREAT \times day, TREAT \times day²), because non-oiled birds were not expected to respond to days post-oiling. The candidate model set of logistic regression models for feeding by externally-oiled birds consisted of all possible combinations of these main effects and interactions, as well as an intercept-only null model, leading to a set of 62 candidate models (Appendix B).

The small sample of observation periods during which feeding occurred in the external-oiling experiment ($n = 76$ observations) precluded consideration of complex models. The set of candidate general linear mixed models for time spent feeding consisted of all possible combinations of the main effects of TREAT, WIND, DIURN, and temp, as well as an intercept-only null model, leading to a set of 16 candidate models (Appendix C).

The effect of external-oiling treatment on maintenance activity was expected to operate through decreased plumage quality and to be additive to the effects of weather and time. Linear and quadratic trends in the response of maintenance activity to external-oiling over days post-oiling were incorporated in models as interactions with TREAT. The set of candidate models for both logistic regression and general linear mixed models was composed of all possible combinations of main effects, TREAT \times day and TREAT \times day² interactions, and an intercept-only null model, leading to a set of 30 candidate models (Appendix D).

Logistic regression models were fit using PROC GENMOD of program SAS (SAS Institute 1999). Violation of the assumption of independent outcomes caused by repeated observations on the same subjects can lead to overdispersion from the binomial distribution and underestimation of variance (McCullagh and Nelder 1989). To assess overdispersion in the data, a variance inflation factor, c , was estimated based on the global model from each candidate set, where \hat{c} was the ratio of the deviance statistic to its degrees of freedom. When $\hat{c} > 1$, quasi-

likelihood estimation (McCullagh and Nelder 1989) and QAIC_c, the quasi-likelihood adjusted calculation of AIC_c, were used; when $\hat{c} \leq 1$, no adjustments were made and model-selection was based on AIC_c (Burnham and Anderson 2002). The goodness-of-fit of the global model in each set of logistic regression models was assessed using a deviance chi-square goodness-of-fit test to test the null hypothesis that the model was adequate (i.e., $P > 0.05$ indicated adequate fit; Ramsey and Schafer 2002). Model-derived estimates of response values for treatment groups were adjusted for average values of the other explanatory variables included in each model and averaged across all models based on Akaike weights. Model-averaged, adjusted mean estimates were back-transformed from the logit scale to estimates of probability.

General linear mixed models were fit using PROC MIXED of program SAS (SAS Institute 1999) and were used to account for correlation among residuals from repeated observations. General linear mixed models structure the correlation among residuals from each subject into a parameterized matrix (Wolfinger 1993, Littell et al. 2000). A parameter for a random between-subject effect also was considered in the covariance structure of the model. For general linear mixed model sets, the best-fitting covariance structure was selected from a set of candidate structures using AIC_c model-selection criteria (Wolfinger 1993, Littell et al 2000). The spatial powers law structure to model decreasing correlation with increasing time between repeated observations, and the compound symmetric structure to

model constant variance-covariance were the candidate residual structures considered (Wolfinger 1993, Littell et al. 2000). The best-fitting covariance structure was incorporated into all fixed effects model structures in the candidate set. The fit of the global general linear mixed model in each candidate set was assessed using a null model likelihood ratio test to test the null hypothesis that the global model did not improve fit over the null model (i.e., $P < 0.05$ indicated adequate fit; Ramsey and Schafer 2002).

Prior to analysis, measurements of the proportion of time spent in a given activity (p) were logit transformed to meet model requirements of constant variance and normal distribution, where:

$$\text{logit } p = \ln[p/(1-p)].$$

Residual plots from the global model and top-ranked models from each candidate model set were used to confirm that model assumptions of normal distribution and constant variance were met; case influence statistics were calculated and examined for influential data points (Ramsey and Schafer 2002). Model-derived estimates of the mean response for each treatment group were adjusted for average values of all other explanatory variables included in the model and averaged across all models based on Akaike weights. Model-averaged, adjusted mean estimates were back-transformed to yield the proportion of time spent in the activity.

Variables included in the top-ranked model(s) for each candidate set ($\Delta\text{AIC} \leq 2.0$) were interpreted as being important to the process being examined (either

probability of occurrence or duration of an activity). Inclusion of oil-dosing treatment in the top model(s) of a candidate set was interpreted as evidence of an oil treatment effect. Summed Akaike weights for explanatory variables were used to judge the importance of the TREAT main effect and the TREAT \times YEAR interaction. Unconditional 95% confidence intervals around model-averaged, adjusted mean estimates of response variables for oil exposure treatments were used to infer differences among treatments.

Results

Effects of Oil Ingestion on Feeding Behavior

Behavioral observations were collected during a total of 820 30-minute observation periods from 39 birds during the 2 winters of the oil ingestion experiment, 482 periods during winter 2000-01 and 338 periods during winter 2001-02. Feeding activity occurred during 68% of all observation periods. The fit of the global logistic regression model to the data was adequate (deviance goodness-of-fit $\chi^2_{807} = 807.9, P = 0.4845$) after adjusting for slight overdispersion ($\hat{c} = 1.25$).

We found no evidence that feeding activity was affected by oil-dosing treatment. The intercept-only null model was selected as best-fitting the data (Table 3.2). Summed Akaike weights for each of the explanatory variables considered in the models were low, indicating that none of the explanatory

Table 3.2. Model-selection statistics from logistic regression and general linear mixed models for feeding and maintenance activities by harlequin ducks in an oil-dosing experiment at the Alaska SeaLife Center, Seward, Alaska during winters 2000-01 and 2001-02. The models best-fit by our data ($\Delta\text{AIC} \leq 2$) are presented.

Response variable	Model ^a	k ^b	Log-likelihood	ΔAIC^c	Model weight
Probability of feeding	Intercept	2	-513.70	0.00	0.20
	YEAR	3	-513.30	1.35	0.10
	TREAT + YEAR + TREAT × YEAR	7	-508.40	1.52	0.09
	DIURN + YEAR	5	-511.20	1.95	0.08
Proportion of time feeding	temp + dayl + WIND + DIURN + YEAR	11	-605.80	0.00	0.30
	dayl + WIND + DIURN + YEAR	10	-606.80	0.01	0.29
	dayl + DIURN + YEAR	8	-609.80	1.88	0.12
Probability of maintenance	temp + TREAT + YEAR + TREAT × YEAR	7	-246.76	0.00	0.38
Proportion of time maintenance	TREAT + DIURN + YEAR	9	-1532.82	0.00	0.16
	DIURN + YEAR	7	-1535.01	0.29	0.14
	temp + TREAT + DIURN + YEAR	10	-1532.69	1.80	0.07
	TREAT + DIURN + YEAR + TREAT × YEAR	11	-1531.72	1.92	0.06

^aSee Methods for explanatory variable abbreviations.

^bNumber of estimated parameters includes +1 for intercept for all models, +1 for the estimate of the variance inflation factor for QAIC_c models, and +3 for parameters in the covariance structure of general linear mixed models (spatial powers law residual structure, random between-subject effect, and variance estimate).

^cSee Results for form of AIC model selection criteria used for each response.

Table 3.3. Variable weights for explanatory variables considered in models describing variation in feeding and maintenance activities by harlequin ducks in an oil-dosing experiment at the Alaska SeaLife Center, Seward, Alaska during winters 2000-01 and 2001-02. Variable weights are Akaike weights summed across all models that included a given variable, and indicate the relative support for that variable. Variables with the greatest relative support are those with variable weights close to 1.0.

Response variable	Variable weight					
	Time of day	Day length	Treatment	Temperature	Wind	Treatment × Year
Probability of feeding	0.288	0.186	0.375	0.247	0.097	0.310
Proportion of time feeding	1.000	0.999	0.294	0.417	0.832	0.203
Probability of maintenance	0.255	0.185	0.890	0.844	0.199	0.609
Proportion of time maintenance	0.723	0.233	0.604	0.233	0.149	0.134

variables considered in the *a priori* logistic regression models were important for explaining variation in the probability of feeding (Table 3.3). Thus the probability of feeding activity by harlequin ducks during an observation period was unrelated to the weather, time, or oil treatment variables considered in our *a priori* models.

When feeding activity occurred during an observation period ($n = 558$ observations from 39 birds), results did not support an oil-dosing effect on the proportion of time spent feeding. The global general linear mixed model for the proportion of time spent in feeding activity adequately fit the data (null model likelihood ratio test $\chi^2_{14} = 292.3$, $P < 0.0001$). The oil-dosing treatment explanatory variable was not included among the 3 models with $\Delta AIC_c \leq 2$ (Table 3.2). Summed Akaike weights for TREAT and the TREAT \times YEAR interaction were low and indicated that these variables did not account for important variation in time spent feeding; day length, time of day, wind speed, and year were supported as important explanatory variables (Table 3.3). Model-averaged parameter estimates (\pm SE) indicated (1) a negative association between time spent feeding and day length (dayl: $-0.002 \pm 4.0E-4$), (2) greater feeding activity during the second year of the study (YEAR: 0.821 ± 0.18), (3) increased feeding through the day (afternoon: 0.22 ± 0.07 , evening: 0.46 ± 0.07), and (4) increased feeding during moderate wind conditions (0.16 ± 0.07). Time spent feeding, however, was not affected by oil-dosing.

Effects of Oil Ingestion on Maintenance Behavior

Maintenance activity occurred during 90% of behavioral observation periods. The probability that maintenance activity would occur during an observation period was related to oil-dosing treatment during the first year of the study, but not during the second year. The global logistic regression model adequately fit the data (deviance goodness-of-fit $\chi^2_{808} = 487.53$, $P = 1.00$) and no evidence of overdispersion was found ($\hat{c} = 0.60$). The TREAT main effect and TREAT \times YEAR interaction both were included in the model selected as best-fitting the data (Table 3.2), and both of these explanatory variables were supported by summed Akaike weights (Table 3.3), indicating the effect of oil-dosing treatment differed between years. Results also indicated the importance of ambient temperature in the model (Table 3.3), which had a model-averaged parameter estimate (\pm SE) of 0.07 ± 0.03 , indicating increased occurrence of maintenance activity at higher ambient temperatures. Probability estimates for maintenance activity in the high- and low-dose treatments during winter 2000-01 were 0.84 (95% CI: 0.78 to 0.90) and 0.86 (95% CI: 0.79 to 0.91), respectively, 10% less than the estimated probability for control birds (0.95, 95% CI: 0.90 to 0.98; Fig. 3.1). Estimates for each treatment during the second winter had highly over-lapping 95% confidence intervals (Fig. 3.1). Thus oil-dosed birds had a lower probability of engaging in maintenance activity than controls during the first year of the study, while no oil-dosing effect was evident during the second year.

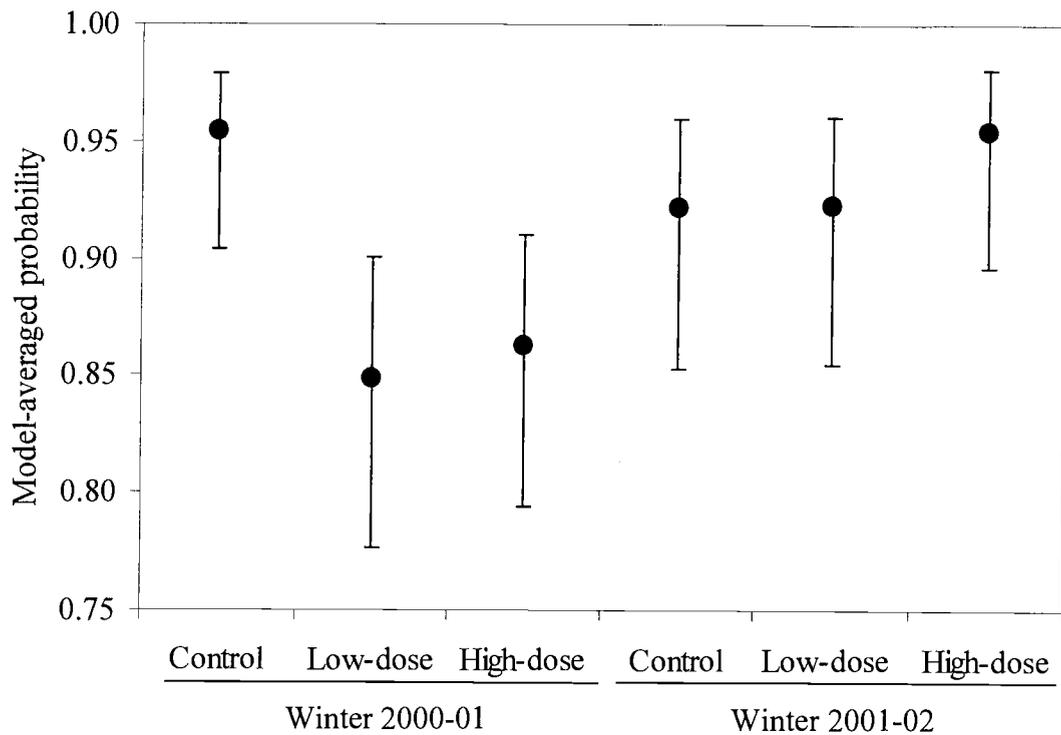


Fig. 3.1. Estimates of the probability of occurrence of maintenance activity during 30-minute observation periods by harlequin ducks in an oil-dosing experiment at the Alaska SeaLife Center, Seward, Alaska during winters 2000-01 and 2001-02. Estimates are adjusted for the effects of covariates and averaged across all considered models based on Akaike weights. Error bars represent 95% confidence intervals.

Results supported an oil-dosing treatment effect on proportion of time spent in maintenance activity, but only for birds in the low-dose treatment during the first year of the study. The global general linear mixed model for the proportion of time spent in maintenance activity showed adequate fit (null model likelihood ratio test $\chi^2_{14} = 57.0, P < 0.0001$). Three of the 4 models with $\Delta AIC_c \leq 2$ included TREAT, and one model included the TREAT \times YEAR interaction (Table 3.2). Summed Akaike weights, however, showed little support for the TREAT \times YEAR interaction, while moderate support was indicated for the TREAT main effect (Table 3.3). The model-averaged parameter estimate (\pm SE) for the effect of YEAR indicated greater time spent in maintenance activity during the second year of the study (0.73 ± 0.22), most likely associated with increased time spent in the water for dive-feeding. Because the TREAT \times YEAR interaction was included among models with $\Delta AIC_c \leq 2$, the proportion of time spent in maintenance activity was estimated for oil-dosing treatments separately in each year. Estimates of the mean proportion of time spent in maintenance activity were similar among oil-dosing treatments in the second year of the study, while estimates for the first year indicated the average time spent in maintenance activity by birds in the low-dose treatment was 48% less than the estimates for birds in the control and high-dose treatments (Fig. 3.2).

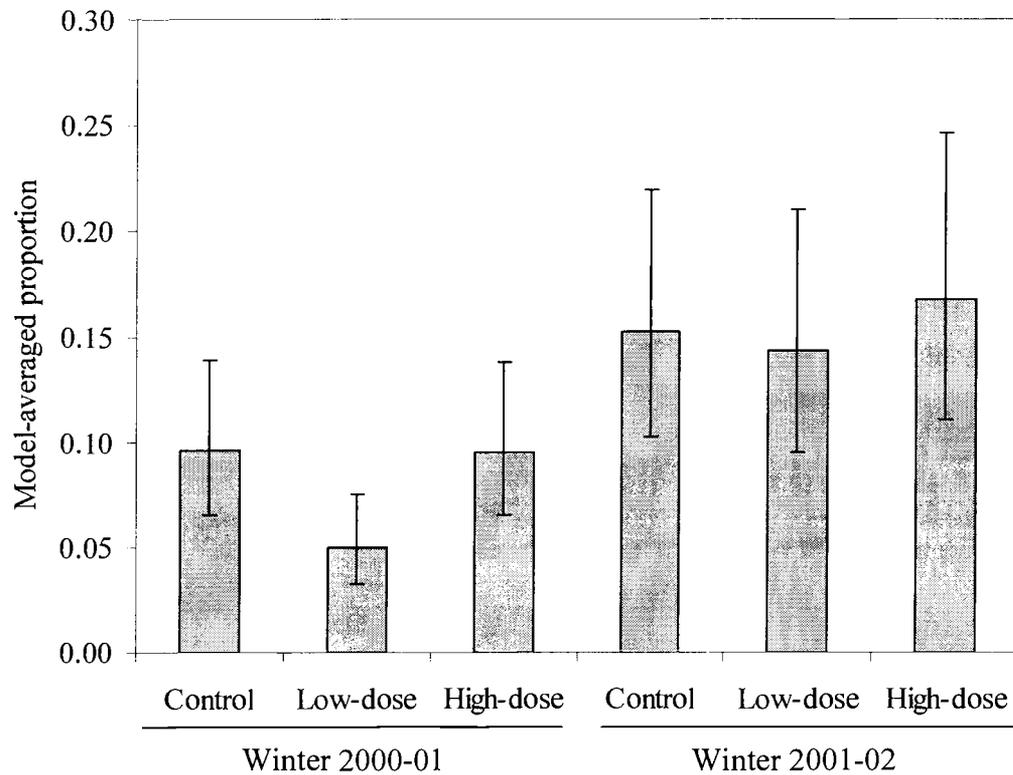


Fig. 3.2. Estimates of the proportion of time spent in maintenance activity by harlequin ducks in an oil-dosing experiment at the Alaska SeaLife Center, Seward, Alaska during winters 2000-01 and 2001-02. Estimates are adjusted for the effects of covariates and averaged across all considered models based on Akaike model weights. Error bars represent 95% confidence intervals.

Effects of Plumage-oiling on Feeding Behavior

Behavioral observations were collected during a total of 160 30-minute observation periods from 16 birds during the plumage-oiling experiment. Feeding activity occurred during 47.5 % of all observation periods. The global logistic regression model for the probability of feeding adequately fit the data (deviance goodness-of-fit $\chi^2_{141} = 141.9, P = 0.4608$) after adjusting for slight overdispersion ($\hat{c} = 1.36$).

Results indicated that the heavy-oiling treatment reduced the probability of feeding activity by birds during an observation period. The TREAT main effect was included in the 2 logistic regression models with $\Delta\text{QAIC}_c \leq 2$ (Table 3.4). Summed Akaike weights for explanatory variables showed strong support for the TREAT main effect (Table 3.5). Estimates of the probability of feeding for each plumage-oiling treatment indicated a 43% reduction in the probability of feeding by birds associated with the heavy-oiling treatment, but no apparent effects associated with light- or moderate-oiling (Fig. 3.3). The probability of feeding by control birds was estimated to be 0.45 (95% CI: 0.29 to 0.84), while the probability of feeding by birds in the heavy-oiling treatment was only 0.21 (95% CI: 0.10 to 0.39); the 95% confidence intervals around these estimates showed only slight overlap, providing strong evidence of a negative effect of the heavy-oiling treatment on the probability of feeding.

Table 3.4. Model-selection statistics from logistic regression and general linear mixed models for feeding and maintenance activities by harlequin ducks in a plumage-oiling experiment at the Alaska SeaLife Center, Seward, Alaska during February-March 2002. The models best-fit by our data ($\Delta\text{AIC} \leq 2$) are presented.

Response variable	Model ^a	k ^b	Log-likelihood	ΔAIC^c	Model weight
Probability of feeding	TREAT	5	-101.29	0.00	0.28
	TREAT + WIND	6	-100.70	1.30	0.15
Proportion of time feeding	TREAT	6	-72.88	0.00	0.16
	WIND	5	-74.15	0.17	0.15
	temp	4	-75.30	0.19	0.14
	DIURN	4	-75.57	0.72	0.11
	TREAT + DIURN	7	-72.44	1.55	0.07
	DIURN + WIND	6	-73.73	1.70	0.07
Probability of maintenance	Intercept	1	-60.28	0.00	0.21
	TREAT	4	-57.39	0.44	0.17
	temp	2	-60.18	1.84	0.09
	DIURN	2	-60.25	1.99	0.08
Proportion of time maintenance	temp	4	-295.42	0.00	0.19
	temp + DIURN	5	-294.73	0.77	0.13
	temp + WIND	6	-293.78	1.05	0.11
	temp + TREAT	7	-292.90	1.51	0.09

^aSee Methods for explanatory variable abbreviations.

^bNumber of estimated parameters includes +1 for intercept for all models, +1 for the estimate of the variance inflation factor for QAIC_c models, and +2 for parameters in the covariance structure of general linear mixed models (compound symmetric residual structure and variance estimate).

^cSee Results for form of AIC model selection criteria used for each response.

Table 3.5. Variable weights for explanatory variables considered in models describing variation in feeding and maintenance activities by harlequin ducks in a plumage-oiling experiment at the Alaska SeaLife Center, Seward, Alaska during February–March 2002. Variable weights are Akaike weights summed across all models that included a given variable, and indicate the relative support for that variable. Variables with the greatest relative support are those with variable weights close to 1.0.

Response variable	Variable weight							
	Time of day	Treatment	Temperature	Wind	Treatment × temperature	Treatment × wind	Treatment × days post-oiling	Treatment × days post-oiling ²
Probability of feeding	0.149	0.978	0.346	0.394	0.069	0.036	0.089	0.039
Proportion of time feeding	0.365	0.388	0.359	0.368	NA	NA	NA	NA
Probability of maintenance	0.261	0.486	0.248	0.171	NA	NA	0.070	0.046
Proportion of time maintenance	0.451	0.361	0.764	0.325	NA	NA	0.006	0.006

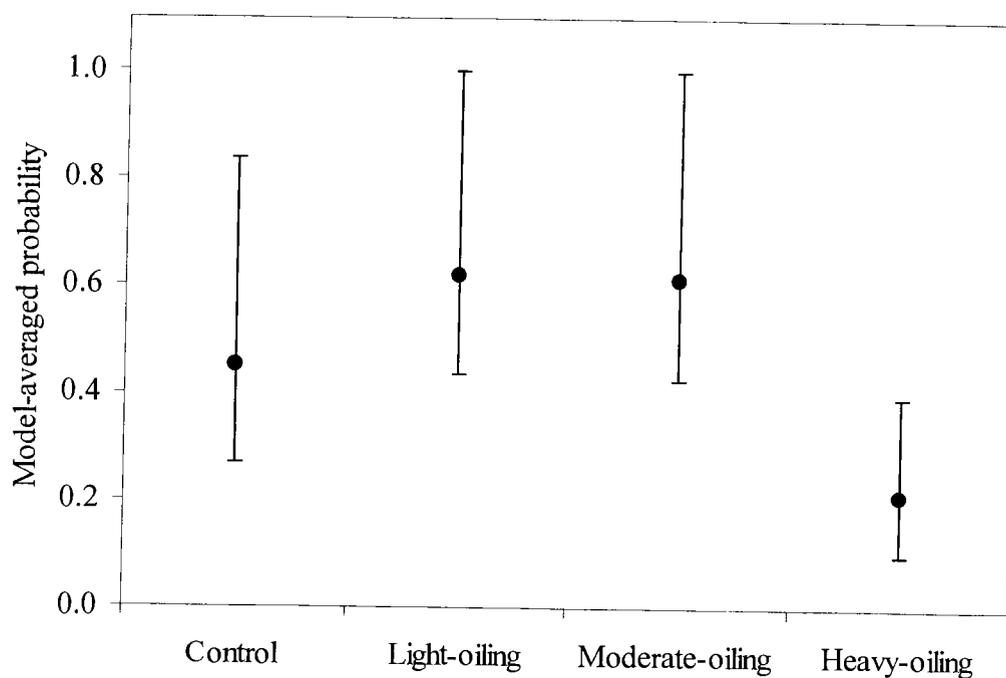


Fig. 3.3. Estimates of the probability of occurrence of feeding activity during 30-minute observation periods by harlequin ducks in a plumage-oiling experiment at the Alaska SeaLife Center, Seward, Alaska during February–March 2002. Estimates are adjusted for the effects of covariates and averaged across all considered models based on Akaike weights. Error bars represent 95% confidence intervals.

When feeding activity was observed during observation periods ($n = 76$ observations from 16 birds), we found evidence of decreased time spent feeding with increased plumage-oiling. The global general linear mixed model for the proportion of time spent feeding by birds in the external-oiling experiment showed adequate fit to the data (null model likelihood ratio test $\chi^2_6 = 16.2$, $P = 0.0127$). The model that included only the TREAT explanatory variable was selected as best-fitting; however, this model received a low Akaike model weight indicating little support (Table 3.4). Five additional models had $\Delta AIC_c \leq 2$, indicating considerable uncertainty in model-selection for this response variable. Summed Akaike weights for the plumage-oiling treatment variable received the greatest amount of support relative to the other explanatory variables considered, although support for all variables was low (Table 3.5). There was, however, a clear trend of decreased mean proportion of time spent feeding with increased external-oiling (Fig. 3.4). The plumage-oiling treatment effect was most evident in birds from the heavy-oiling treatment, which had an estimated mean proportion of time spent feeding of 0.042 (95% CI: 0.026 to 0.066), 43% less than the estimated mean proportion of time spent feeding by birds in the control treatment (0.074, 95% CI: 0.053 to 0.102; Fig. 3.4).

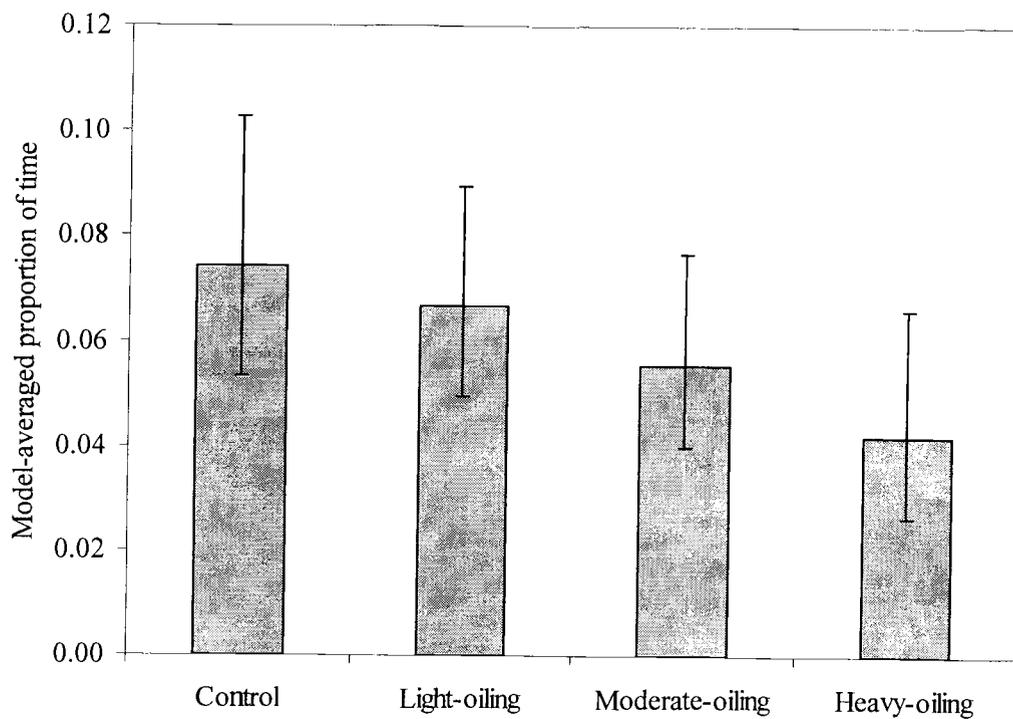


Fig. 3.4. Estimates of the proportion of time spent in feeding activity by harlequin ducks in a plumage-oiling experiment at the Alaska SeaLife Center, Seward, Alaska during February–March 2002. Estimates are adjusted for the effects of covariates and averaged across all considered models based on Akaike model weights. Error bars represent 95% confidence intervals.

Effects of Plumage-oiling on Maintenance Behavior

Results indicated little support for a plumage-oiling effect on the probability of occurrence of maintenance activity during an observation period. Maintenance activity occurred during 87% of behavioral observation periods. The global logistic regression model for the probability of maintenance activity indicated adequate fit (deviance goodness-of-fit $\chi^2_{147} = 107.0$, $P = 0.9946$), with no evidence of overdispersion in the data ($\hat{c} = 0.73$). The intercept-only null model and the model including only the TREAT explanatory variable had $\Delta AIC_c \leq 2$ (Table 3.4), indicating that the data did not convincingly support a plumage-oiling effect. Summed Akaike weights for explanatory variables indicated moderate support for a plumage-oiling treatment effect, and little support for the other explanatory variables considered (Table 3.5). Estimates of the probability of maintenance activity by lightly-oiled (0.896, 95% CI: 0.718 to 0.967), and moderately-oiled birds (0.882, 95% CI: 0.735 to 0.953) were greater than the estimate for control birds (0.778, 95% CI: 0.600 to 0.891); however, 95% confidence intervals around these estimates overlapped considerably (Fig. 3.5). The estimated probability of maintenance activity for heavily-oiled birds (0.953, 95% CI: 0.822 to 1.00) was suggestive of an increased incidence of maintenance activity compared to control birds (Fig. 3.5).

Results provided little support for the hypothesis that the plumage-oiling treatment affected the proportion of time spent in maintenance activity. The global

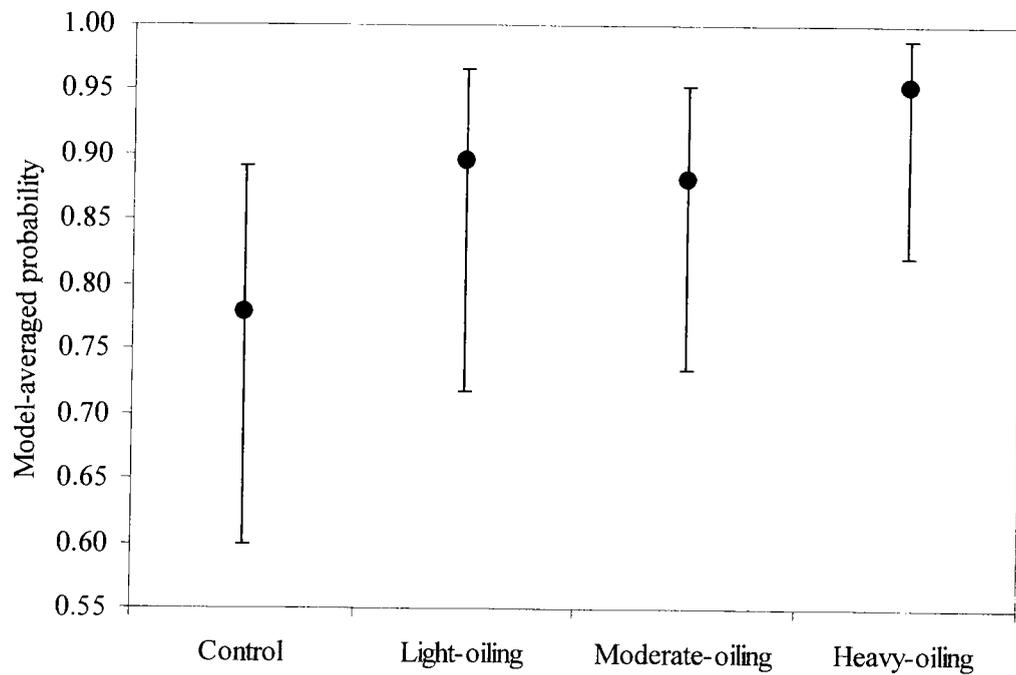


Fig. 3.5. Estimates of the probability of occurrence of maintenance activity during 30-minute observation periods by harlequin ducks in a plumage-oiling experiment at the Alaska SeaLife Center, Seward, Alaska during February–March 2002. Estimates are adjusted for the effects of covariates and averaged across all considered models based on Akaike weights. Error bars represent 95% confidence intervals.

general linear mixed model for proportion of time spent in maintenance activity indicated adequate fit to the data (null model likelihood-ratio-test $\chi^2_{12} = 21.5$, $P = 0.0387$). Of the 4 models with $\Delta AIC_c \leq 2$, only one included the explanatory variable for plumage-oiling treatment (Table 3.4). Summed Akaike weights indicated little support for an effect of plumage-oiling (Table 3.5). The model-averaged estimate of the mean proportion of time spent in maintenance activities by control birds (0.142, 95% CI: 0.07 to 0.27) was similar to that of the lightly-oiled birds (0.121, 95% CI: 0.065 to 0.213; Fig. 3.6). The mean proportion of time spent in maintenance activities for moderately-oiled birds (0.276, 95% CI: 0.162 to 0.427) and heavily-oiled birds (0.227, 95% CI: 0.131 to 0.365) were 48% and 37% greater, respectively, than the estimate for control birds; however, the large variation around these estimates prevents strong conclusions from being made (Fig 3.6).

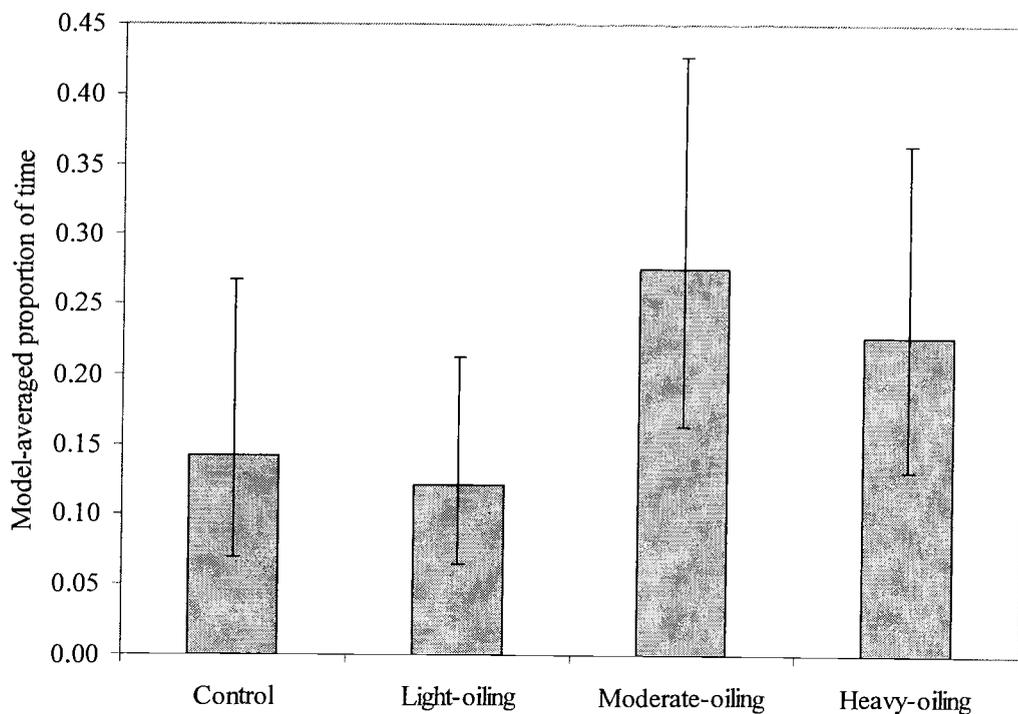


Fig. 3.6. Estimates of the proportion of time spent in maintenance activity by harlequin ducks in a plumage-oiling experiment at the Alaska SeaLife Center, Seward, Alaska during February–March 2002. Estimates are adjusted for the effects of covariates and averaged across all considered models based on Akaike model weights. Error bars represent 95% confidence intervals

Discussion

Effects of Oil Ingestion on Behavior

We observed no overt signs of intoxication in harlequin ducks dosed with weathered Prudhoe Bay crude oil under the dosing regimes and conditions of captivity in this study. Other species of waterfowl have shown similar tolerance of oil ingestion in captivity (Coon and Dieter 1981, Rattner 1981, Stubblefield et al. 1995, Boehm et al. 1996), although the toxicity of ingested oil may vary among species, crude oils, and extent of weathering (Leighton 1993). Behavioral differences among birds in oil-dosed and control treatments were detected, but these differences were not consistent between the 2 years of the experiment, nor was there evidence of a dose-response effect. Our results, therefore, provide little support for the hypothesis that oil ingestion causes changes in the feeding and maintenance components of the time-activity budget of captive harlequin ducks.

Oil ingestion has been hypothesized to cause increased feeding by (1) reducing digestive efficiency (Eastin and Murray 1981, Ormseth and Ben-David 2000); (2) increasing resting energy requirements through the chronic induction of detoxification, excretion, and repair mechanisms (Callow 1991); or (3) triggering a generalized physiological stress response (Holmes et al. 1978, 1979). Oil-dosed harlequin ducks in captivity showed no evidence of increased feeding activity. Additionally, food consumption rate, which was measured in a companion study, showed no differences among treatments (D. Esler, unpublished data). Ben-David

et al. (2000) found that oil-dosing in captive river otters caused anemia and reduced dive times while foraging. During the second year of the present study, we examined feeding activity in captive harlequin ducks at the scale of the proportion of total feeding time spent diving and found no differences across oil-dosing treatments ($\chi^2_2 = 0.685$, $P = 0.7099$). This result was supported by a related study of blood parameters during the first year of dosing, which found no differences in packed cell volume, an indicator of damage to red blood cells, among oil-dosing treatments (K. Trust, U.S. Fish and Wildlife Service, pers. comm.).

Oil dosing effects on maintenance activity were likely indirect. For example, if oil ingestion caused increased lethargy, as was observed in oil-dosed sandhill cranes (Flemming et al. 1982), reallocation of time might be at the expense of maintenance activity. Time spent in maintenance activity by birds in the low-dose treatment during the first year of the present study was negatively correlated with time spent in resting behavior ($r = -0.39$). This effect may have been related to either the lower dosing frequency, the higher dose per dosing, and (or) the lower proportion of time spent in maintenance activity in the first year, compared to the second year of the study. There was no effect, however, on time spent in maintenance activity for birds in the high-dose treatment. These results do not strongly support the hypothesis that oil-dosing affects maintenance activity, given the absence of a high-dose effect on time spent in maintenance activity, the

inconsistency of the treatment effects between years, and the absence of observable differences in plumage quality among treatment groups.

The absence of a dose-response effect on time-activity budgets of captive harlequin ducks may be related to excretion of some portion of the dose of crude oil in feces, instead of absorption of the oil in the digestive tract. Birds and mammals fed doses of crude oil have been shown to excrete 45-85% of the doses in feces, which may confound dose-response effects (McEwan and Whitehead 1980, Eastin and Murray 1981, Ormseth and Ben-David 2000). Excretion of ingested oil in feces was observed soon after dosing during the 60-90 minute holding period in both years of this study, and in both oil-dose treatments. Rapid excretion may serve as an effective mechanism for mitigating the toxicity of ingested oil (McEwan and Whitehead 1980, Ormseth and Ben-David 2000). In the present study, levels of hepatic CYP1A in birds at the end of the dosing experiment were elevated for both oil-dosed treatments relative to controls (D. Esler, unpublished data), indicating that some oil was absorbed and detoxified at both dosages. The proportion of oil that was defecated after dosing, however, was not measured.

Oil exposure differed qualitatively between the dosing regime administered in captivity and the oil exposure likely experienced by harlequin ducks in oil-contaminated areas of PWS. Contamination of benthic invertebrates (Fukuyama 2000, Carls et al. 2001) makes ingestion of contaminated prey a likely source of exposure for harlequin ducks in the wild. Such exposure would occur in the form

of PAHs incorporated in prey tissue, which may lead to effects different from those caused by ingestion of whole, weathered crude oil. In the present study, we found ingestion of weathered crude oil by harlequin ducks in captivity to cause rapid defecation of oil prior to absorption. PAHs incorporated into the tissues of invertebrate prey likely would not induce such a voiding mechanism and may result in higher assimilation rates for PAHs. Additionally, given the high winter site philopatry of harlequin ducks, birds wintering on oiled areas are likely to experience exposure not only within one winter season, but across multiple winters (Esler et al. 2000*b*). Such chronic exposure creates the potential for cumulative damage over multiple years (Callow 1991), and these effects may not be reproduced by one season of oil ingestion in birds previously unexposed to oil.

The level of residual oil ingested by harlequin ducks in PWS is unknown. The dosing regime used in this study was intended to bracket a range of potential exposures. The low-dose treatment administered in this study was meant to simulate exposure as it may occur in oiled areas of PWS many years after the oil spill, while the high-dose treatment was representative of the level of exposure that would occur only in the immediate wake of an oil spill, and therefore most likely to affect behavior. This range of exposure induced hepatic CYP1A in captive birds to levels similar to those documented in wild harlequin ducks from oiled portions of PWS (D. Esler, unpublished data). The amount of ingested oil that was assimilated and which induced the measured levels of hepatic CYP1A was likely much less

than the amount fed to the birds because not all oil was absorbed and detoxified (i.e., some oil was defecated). Despite induction of hepatic CYP1A, no consistent behavioral effects from the dosing treatments were found, suggesting that induction of detoxification mechanisms does not necessarily imply corresponding behavioral effects, such as increased feeding activity (Jenssen 1989, Calow 1991). CYP1A may, therefore, be a more sensitive indicator of exposure to PAHs than behavior, but may not be indicative of negative effects, unless negative effects result from a mechanism not induced under the conditions of captivity.

Effects of Plumage-oiling on Behavior

Our results support the hypothesis that plumage-oiling causes changes in harlequin duck behavior in captivity. There was a clear dose-response trend in the proportion of time spent feeding by harlequin ducks in the plumage-oiling experiment, with less feeding by more heavily-oiled birds. The effect of plumage-oiling was most evident in the heavy-oiling treatment group, whose estimated proportion of time spent feeding was 43% less than that of controls. The decrease in proportion of time spent feeding likely resulted from reduced time spent in the water because dive-feeding with oiled plumage causes high rates of heat loss (Jenssen and Ekker 1990, Jenssen and Ekker 1991*a, b*). Plumage-oiling increases thermal conductance of wet plumage, which raises the lower critical temperature at which birds must increase their metabolic rate in order to thermoregulate (Hartung

1967, McEwan and Koelink 1973, Jenssen and Ekker 1990, 1991*a, b*). The effects of plumage-oiling on waterfowl can be dramatic; heat loss in common eiders exposed to 12.5 mL of crude oil was increased by 360% while resting in water at 5°C (Jenssen and Ekker 1990). The effects of plumage-oil on captive harlequin ducks were greatest in the heavy-oiling treatment (5 mL of crude oil), which reduced both the probability of feeding during an observation period and the amount of time spent feeding.

To maintain body temperature, externally-oiled birds with wet plumage must increase their resting metabolic rate in proportion to the degree of plumage-oiling (Hartung 1967, McEwan and Koelink 1973, Jenssen and Ekker 1991). In contrast, common eiders resting on land with oiled but dry plumage showed no evidence of higher heat loss (Jenssen and Ekker 1990). It seems likely that externally-oiled harlequin ducks spent less time feeding to reduce time in the water and limit wetting of their plumage. Common eiders showed a similar increase in time spent on shore after exposure to a 2.5 mL mixture of crude oil and oil-dispersant (Ekker et al. 1989).

Increased resting metabolic rate would carry an associated increase in energy requirement, yet externally-oiled harlequin ducks in captivity reduced their feeding time. Despite reduced feeding time, however, no differences in food consumption rate were found among treatment groups of externally-oiled birds (D. Esler, unpublished data), indicating that externally-oiled harlequin ducks increased

their foraging efficiency (i.e., increased the quantity of food consumed per unit feeding time). Despite this change in behavior, externally-oiled harlequin ducks lost body mass over the experimental oiling period (D. Esler, unpublished data), indicating that behavioral adaptations to mitigate the costs of thermoregulation were not sufficient to compensate for the greater heat loss associated with plumage-oiling.

Time spent preening by oiled shorebirds at the site of an oil spill increased with the percentage of the plumage that was oiled (Burger 1997). Heat production by oiled common eiders was higher 1-day after exposure compared to immediately following exposure, and was attributed to preening of oil deeper into plumage (Jenssen and Ekker 1991*b*). Oiled sanderlings were found to spread oil by preening, causing a 10% increase in the percentage of the plumage covered with oil following exposure (Burger and Tsipoura 1998). Although variation in the maintenance activity of birds within plumage-oiling treatment groups was large, estimates of both the probability of engaging in maintenance activity during an observation period and the proportion of time spent in maintenance activity taken together were suggestive of oiling effects at the moderately- and heavily-oiled levels. Estimates of the proportion of time spent in maintenance activities suggest a threshold for effect at the moderately-oiled level (2.5 mL of crude oil). Plumage-oiling at the lightly-oiled treatment level did not cause feathers to become matted with oil, whereas at the moderately- and heavily-oiled treatment levels oil

penetrated below the surface of the feathers and caused matting and loss of water repellency. Moderately- and heavily-oiled treatments produced similar increases in proportion of time spent in maintenance activity, although the differences in exposure did lead to differences in the extent of external-oiling based on visual appearance.

The large variation in maintenance activity exhibited by birds in each plumage-oiling treatment may be related to differences in the degree and pattern of oiling. Although the majority of oil administered to birds was absorbed by the plumage, the pattern of the oiling in each bird was dependent on the activity level of the bird during the exposure period. Differences in plumage oiling within a treatment group would contribute to variation in maintenance activity, particularly with a relatively small sample size of subjects.

Reduction of time spent in critical activities may have negative consequences for fitness during energetically demanding periods of the annual cycle (Burger 1997). Increased time spent in maintenance activities caused by plumage-oiling, even at low levels and in the absence of acute mortality, would reduce the time available for other activities such as feeding. For harlequin ducks, reliance on dive-feeding in nearshore habitats not only increases the risk of exposure to oil, but also increases the severity of the effects of plumage-oiling, which are greater in birds that must spend time in the water to feed (Jenssen and Ekker 1991*b*). In addition, the small body size, high surface area to volume ratio,

and low thermal conductance of harlequin ducks compared to other waterfowl (D. Esler, unpublished data) makes the species especially vulnerable to the effects of plumage-oiling (Jenssen and Ekker 1991*b*). Although externally-oiled harlequin ducks adjusted their behavior to compensate for much of the effect of plumage-oiling in captivity, oiled birds did lose body mass during the oiling period (D. Esler, unpublished data), and thus were in negative energy balance. Similar behavioral alterations would almost certainly be ineffective in the wild where foraging requires considerable time in the water.

Behavioral Constraints on Population Recovery

Toxicological studies conducted on captive animals are limited in the inferences that may be extended to wild populations (Hienz 1989). In this study, we sought to determine effects of oil exposure on the behavior of harlequin ducks in captivity that may underlie population-level effects documented in the wild (Esler et al. 2000*b*). Environmental conditions experienced by wild harlequin ducks wintering in Alaska, however, differ greatly from those experienced in captivity, where food was high quality and required minimal foraging effort. This distinction was obvious in the difference between time spent feeding by harlequin ducks wintering in the Aleutian Islands (> 80% of the diurnal period in females during mid-winter; Fischer and Griffin 2000), and time spent feeding by harlequin ducks in captivity (< 10%). This difference in ecological context has major

implications for detecting effects of contaminants on time-activity budgets in captivity, given that environmental conditions may play an important role in toxicity (Gordon 2003). For example, if oil ingestion induced detectable effects on harlequin duck behavior only under conditions of additive stress (Holmes et al. 1978, 1979), such effects may not have been induced in captivity, which was clearly a less demanding environment than the wild.

Based on our results, external exposure to residual oil may contribute to reduced survival in harlequin ducks wintering in contaminated areas of Prince William Sound if residual oil is being released into the water column where it can be encountered by wildlife. Residual EVOS oil documented in 2001 was found in the mid- and lower-intertidal zones, buried below the sediment surface where much of it remained only moderately weathered (Short et al. 2004). Additionally, elevated hepatic CYP1A levels in harlequin ducks from oiled areas are a reliable indicator that continued exposure to PAHs occurred as many as 9 years after the EVOS (Trust et al. 2000). The route of chronic exposure to residual oil in harlequin ducks, however, is not known and may be occurring through ingestion of contaminated prey, external exposure, or a combination of both.

The extent to which residual EVOS oil trapped in sediments is released into the water column is not known. External exposure of harlequin ducks to residual oil in PWS has not been investigated, although oil was detected on the pelage of river otters from oiled areas 8 years after the EVOS (Duffy et al. 1999). Future

research evaluating the prevalence of residual EVOS oil in the water column, as well as on the plumage of harlequin ducks from oiled areas of PWS, would help evaluate the hypothesis that long-term exposure to residual oil is occurring through plumage-oiling. If external exposure is occurring, the behavioral responses to external oiling documented in captive harlequin ducks would most likely be untenable under natural conditions that require harlequin ducks to spend a high proportion of time in the water to feed. Prolonged exposure to water in externally-oiled harlequin ducks could result in excessive heat loss and hypothermia, or force birds to roost on shore and forego feeding, resulting in starvation. Therefore, we conclude that if external exposure to oil occurred at levels high enough to penetrate the plumage, plumage-oiling may have contributed to reduced winter survival of harlequin ducks in PWS by reducing feeding activity.

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CHAPTER 4

CONCLUSIONS

Daniel J. Rizzolo

Results from this thesis suggest that reduced feeding due to plumage-oiling and absence of nocturnal foraging in winter may have contributed to the lack of harlequin duck population recovery from the 1989 *Exxon Valdez* oil spill (EVOS) in oiled areas of Prince William Sound (PWS). I found that the foraging strategy of harlequin ducks during winter apparently does not include nocturnal foraging at the northern extent of their range. This finding agrees with the conclusion of Goudie and Ankney (1986) that harlequin ducks have little flexibility to increase feeding time in winter, which could affect survival during periods of energetic stress. I found that plumage-oiling reduced feeding activity by harlequin ducks in captivity. Reduced feeding activity in the wild may result in negative energy balance and, consequently, increased mortality. These results suggest that behavioral changes in response to plumage-oiling may have contributed to the reduced survival of harlequin ducks in PWS documented by Esler et al. (2000), if residual EVOS oil was entering the water column in contaminated areas.

The association between the apparent absence of nocturnal foraging by harlequin ducks documented in this study and the sensitivity of this species to disturbances on its wintering grounds illustrates how behavioral ecology can influence the vulnerability of species to contaminants. Behavior can influence the probability of encountering contaminants present in the environment, as well as the ability to resist negative effects of such exposure (Pulliam 1994). The use of nearshore habitats by harlequin ducks, as well as their reliance on benthic invertebrate prey and strong winter philopatry, increases the probability that

harlequin ducks in oiled areas of PWS will encounter residual oil. The absence of nocturnal foraging by harlequin ducks may reduce their ability to compensate for disturbances that result in increased maintenance energy requirements and (or) affect foraging behavior, such as contamination of plumage by oil. Behavioral ecology should be used as a criterion for predicting vulnerability of species to disturbances, as well as identifying appropriate species for monitoring. Attributes of harlequin ducks make them an appropriate species for monitoring the effects of disturbances in nearshore marine environments.

Results of oil ingestion experiments indicated no clear oil dose-related alterations in feeding or maintenance activities of captive harlequin ducks. This result suggests that ingestion of weathered Prudhoe Bay crude oil, under the experimental conditions described in Chapter 3, does not compromise the behavioral performance of harlequin ducks, and does not provide support for the hypothesis that ingestion of residual oil contributed to lower survival of wild birds in PWS. The lack of behavioral response to oil ingestion may be related to defecation of a portion of orally-administered oil prior to assimilation, in addition to detoxification by CYP1A of oil that was assimilated; both of these processes excrete weathered crude oil from the body before physiological damage can occur. A caveat to this result, however, is that differences in the conditions of crude oil ingestion in captivity and crude oil ingestion in the wild make comparisons problematic. For example, experiments using ingestion of weathered Prudhoe Bay crude oil cannot address the potential effects of polycyclic aromatic hydrocarbons

(PAHs) accumulated in the tissue of invertebrate prey and consumed as food over extended periods. Future work investigating the behavioral and physiological effects of the ingestion of PAHs administered either in contaminated invertebrates or directly would help evaluate this hypothesis. This caveat emphasizes that the application of inferences from experiments on captive subjects to wild populations must be done cautiously. Controlled, randomized experiments, however, offer the strength of inferring cause and effect relationships.

Quantifying differences in behavior is inherently difficult given that behavior is adaptive and context-dependent. Thus, detecting subtle toxic effects on behaviors with ecological relevance is challenging (Peakall 1996). The behavioral experiments described in this thesis focused on activities important to wintering harlequin ducks and, therefore, effects on these activities are relevant to survival outside of captivity. Time-activity budgets, however, are a coarse-scale estimate of behavior and may not detect fine-scale changes (Heath et al. 2004). Nevertheless, the sampling method and analytical approach used in this study detected changes in harlequin duck time-activity budgets. For example, I found that time spent feeding increased between years in association with changes to feeding protocol. Effects of plumage-oiling on feeding activity also were detected, despite the relatively small sample of repeated observations and the large range of variation in behaviors. Thus, in this situation, time-activity budgets proved to be a useful tool for quantifying effects of contaminants on behavior and may be used to evaluate effects on the probability of occurrence of an activity, as well as the duration of

time spent in the activity. This approach could be complemented by examining finer scale behavior. For example, measuring intake rates of prey using dive-tank observations might detect subtle effects not evident using solely a coarse-scale approach, such as time-activity budgets. Furthermore, controlling important covariates may also bring greater resolution to results by, for example, controlling ambient temperature and photoperiod duration.

Contamination of plumage by residual oil as a mechanism contributing to reduced survival of harlequin ducks in PWS is not dependent on the toxicity of the residual oil, which has been a topic of some contention (Rice et al. 2003, Page et al. 2003). A recent study of lingering oil in PWS concluded that EVOS oil was the largest reservoir of biologically available PAHs on beaches oiled by the spill, and that lingering oil remained a risk for species dependent on these areas (Short et al. 2004). Uncertainty regarding the route of long-term exposure to residual oil in harlequin ducks demonstrates the need to better understand the availability of residual oil to biota in oiled areas of PWS. If residual *Exxon Valdez* oil sequestered in beach sediments enters the water column where it may be encountered by harlequin ducks, such external exposure may lead to reduced feeding activity, which, in turn, may compromise survival. Further, behavioral effects of plumage oiling in light of the prevalence of oil contamination in coastal areas (NRC 2003) raises concerns that chronic, low-level external exposure to oil in birds may have adverse effects and warrants additional research.

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APPENDICES

Appendix A. List of 41 *a priori* candidate model structures used to model the probability of occurrence of feeding and maintenance activities during behavioral observation periods (logistic regression), and the proportion of time spent in feeding and maintenance activities when exhibited (general linear mixed models) by oil-dosed harlequin ducks.

Model No.	Model Structure ^a
1.	Intercept
2.	YEAR
3.	temp + YEAR
4.	dayl + YEAR
5.	TREAT + YEAR
6.	temp + dayl + YEAR
7.	WIND + YEAR
8.	DIURN + YEAR
9.	temp + TREAT + YEAR
10.	temp + WIND+ YEAR
11.	temp + DIURN + WIND
12.	temp + DIURN + YEAR
13.	dayl + WIND + YEAR
14.	dayl + DIURN + YEAR
15.	temp + dayl + TREAT + YEAR
16.	TREAT + YEAR + TREAT × YEAR
17.	TREAT + WIND + YEAR
18.	TREAT + DIURN + WIND
19.	temp + dayl + WIND + YEAR
20.	WIND + DIURN + YEAR
21.	temp + TREAT + WIND + YEAR
22.	temp + TREAT + DIURN + YEAR

Appendix A (continued).

Model No.	Model Structure ^a
23.	temp + TREAT + YEAR + TREAT × YEAR
24.	dayl + TREAT + WIND + YEAR
25.	dayl + TREAT + DIURN + YEAR
26.	dayl + TREAT + YEAR + TREAT × YEAR
27.	temp + WIND + DIURN + YEAR
28.	dayl + WIND + DIURN + YEAR
29.	temp + dayl + TREAT + WIND + YEAR
30.	TREAT + WIND + DIURN + YEAR
31.	TREAT + WIND + YEAR + TREAT × YEAR
32.	TREAT + DIURN + YEAR + TREAT × YEAR
33.	temp + dayl + WIND + DIURN + YEAR
34.	temp + TREAT + WIND + DIURN + YEAR
35.	temp + TREAT + WIND + YEAR + TREAT × YEAR
36.	temp + TREAT + WIND + DIURN + YEAR
37.	dayl + TREAT + WIND + YEAR + TREAT × YEAR
38.	dayl + TREAT + DIURN + YEAR + TREAT × YEAR
39.	temp + dayl + TREAT + WIND + DIURN + YEAR
40.	dayl + TREAT + WIND + DIURNAL + YEAR + TREAT × YEAR
41.	temp + dayl + TREAT + WIND + DIURN + YEAR + TREAT × YEAR

^aExplanatory variables: dayl = day length (minutes of photoperiod), DIURN = diurnal period (morning, afternoon, evening), temp = ambient temperature (°C), TREAT = oil-dosing treatment (control, low-dose, high-dose), WIND = wind speed (light, moderate, high), YEAR = year of experiment (winter 2000-01, winter 2001-02).

Appendix B. List of 62 *a priori* candidate model structures used to model the probability of occurrence of feeding activity during behavioral observation periods (logistic regression) by externally-oiled harlequin ducks.

Model No.	Model Structure ^a
1.	Intercept
2.	DIURN
3.	temp
4.	WIND
5.	temp + DIURN
6.	temp + WIND
7.	WIND + DIURN
8.	temp + WIND + DIURN
9.	TREAT
10.	TREAT + DIURN
11.	TREAT + temp
12.	TREAT + WIND
13.	TREAT + temp + DIURN
14.	TREAT + temp + WIND
15.	TREAT + WIND + DIURN
16.	TREAT + temp + WIND + DIURN
17.	TREAT + day + TREAT × day
18.	TREAT + temp + TREAT × temp
19.	TREAT + WIND + TREAT × WIND
20.	TREAT + day + day ² + TREAT × day ²
21.	TREAT + DIURN + day + TREAT × day
22.	TREAT + temp + day + TREAT × day
23.	TREAT + temp + DIURN + TREAT × temp

Appendix B (continued).

Model No.	Model Structure ^a
24.	TREAT + temp + WIND + TREAT × temp
25.	TREAT + temp + WIND + TREAT × WIND
26.	TREAT + WIND + day + TREAT × day
27.	TREAT + WIND + DIURN + TREAT × WIND
28.	TREAT + DIURN + day + day ² + TREAT × day ²
29.	TREAT + temp + day + day ² + TREAT × day ²
30.	TREAT + temp + DIURN + day + TREAT × day
31.	TREAT + temp + WIND + day + TREAT × day
32.	TREAT + temp + WIND + DIURN + TREAT × temp
33.	TREAT + temp + WIND + DIURN + TREAT × WIND
34.	TREAT + WIND + day + day ² + TREAT × day ²
35.	TREAT + WIND + DIURN + day + TREAT × day
36.	TREAT + temp + DIURN + day + day ² + TREAT × day ²
37.	TREAT + temp + WIND + day + day ² + TREAT × day ²
38.	TREAT + temp + WIND + DIURN + day + TREAT × day
39.	TREAT + WIND + DIURN + day + day ² + TREAT × day ²
40.	TREAT + temp + day + TREAT × temp + TREAT × day
41.	TREAT + temp + WIND + DIURN + day + day ² + TREAT × day ²
42.	TREAT + temp + WIND + TREAT × temp + TREAT × WIND
43.	TREAT + WIND + day + TREAT × WIND + TREAT × day
44.	TREAT + temp + day + day ² + TREAT × temp + TREAT × day ²
45.	TREAT + temp + DIURN + day + TREAT × temp + TREAT × day
46.	TREAT + temp + WIND + day + TREAT × temp + TREAT × day
47.	TREAT + temp + WIND + day + TREAT × WIND + TREAT × day

Appendix B (continued).

Model No.	Model Structure ^a
48.	TREAT + temp + WIND + DIURN + TREAT × temp + TREAT × WIND
49.	TREAT + WIND + day + day ² + TREAT × WIND + TREAT × day ²
50.	TREAT + WIND + DIURN + day + TREAT × WIND + TREAT × day
51.	TREAT + temp + DIURN + day + day ² + TREAT × temp + TREAT × day ²
52.	TREAT + temp + WIND + day + day ² + TREAT × temp + TREAT × day ²
53.	TREAT + temp + WIND + day + day ² + TREAT × WIND + TREAT × day ²
54.	TREAT + temp + WIND + DIURN + day + TREAT × temp + TREAT × day
55.	TREAT + temp + WIND + DIURN + day + TREAT × WIND + TREAT × day
56.	TREAT + WIND + DIURN + day + day ² + TREAT × WIND + TREAT × day ²
57.	TREAT + temp + WIND + DIURN + day + day ² + TREAT × temp + TREAT × day ²
58.	TREAT + temp + WIND + DIURN + day + day ² + TREAT × WIND + TREAT × day ²
59.	TREAT + temp + WIND + day + TREAT × temp + TREAT × WIND + TREAT × day
60.	TREAT + temp + WIND + day + day ² + TREAT × temp + TREAT × WIND + TREAT × day ²
61.	TREAT + temp + WIND + DIURN + day + TREAT × temp + TREAT × WIND + TREAT × day

^aExplanatory variables: day = days post-oiling (continuous), DIURN = diurnal period (afternoon, evening), temp = ambient temperature (°C), TREAT = plumage-oiling treatment (control, light-, moderate-, heavy-oiling), WIND = wind speed (light, moderate/high).

Appendix C. List of 16 *a priori* candidate model structures used to model the proportion of time spent feeding (general linear mixed models) by externally-oiled harlequin ducks.

Model No.	Model Structure ^a
1.	Intercept
2.	DIURN
3.	temp
4.	WIND
5.	DIURN + temp
6.	TREAT
7.	DIURN + WIND
8.	WIND + temp
9.	TREAT + DIURN
10.	TREAT + temp
11.	DIURN + WIND + temp
12.	TREAT + WIND
13.	TREAT + DIURN + temp
14.	TREAT + DIURN + WIND
15.	TREAT + WIND + temp
16.	TREAT + DIURN + WIND + temp

^aExplanatory variables: DIURN = diurnal period (afternoon, evening), temp = ambient temperature (°C), TREAT = plumage-oiling treatment (control, light-, moderate-, heavy-oiling), WIND = wind speed (light, moderate, high).

Appendix D. List of 30 *a priori* candidate model structures used to model the probability of occurrence of maintenance activity during behavioral observation periods (logistic regression), and the proportion of time spent in feeding and maintenance activities when exhibited (general linear mixed models) by externally-oiled harlequin ducks.

Model No.	Model Structure ^a
1.	Intercept
2.	DIURN
3.	temp
4.	temp + DIURN
5.	WIND
6.	temp + WIND
7.	TREAT
8.	WIND + DIURN
9.	temp + WIND + DIURN
10.	TREAT + DIURN
11.	TREAT + temp
12.	TREAT + temp + DIURN
13.	TREAT + WIND
14.	TREAT + temp + WIND
15.	TREAT + WIND+ DIURN
16.	TREAT + day + TREAT × day
17.	TREAT + temp + WIND + DIURN
18.	TREAT + day + day ² + TREAT × day ²
19.	TREAT + DIURN + day + TREAT × day
20.	TREAT + temp + day + TREAT × day
21.	TREAT + DIURN + day + day ² + TREAT × day ²
22.	TREAT + temp + day + day ² + TREAT × day ²

Appendix D (continued).

Model No.	Model Structure
23	TREAT + WIND + day + TREAT × day
24.	TREAT + temp + WIND + day + TREAT × day
25.	TREAT + WIND + day + day ² + TREAT × day ²
26.	TREAT + WIND + DIURN + day + TREAT × day
27.	TREAT + temp + WIND + day + day ² + TREAT × day ²
28.	TREAT + temp + WIND + DIURN + day + TREAT × day
29.	TREAT + WIND + DIURN + day + day ² + TREAT × day ²
30.	TREAT + temp + WIND + DIURN + day + day ² + TREAT × day ²

^aExplanatory variables: day = days post-oiling (continuous), DIURN = diurnal period (afternoon, evening), temp = ambient temperature (°C), TREAT = plumage-oiling treatment (control, light-, moderate-, heavy-oiling), WIND = wind speed (light, moderate, high).