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Effects of the Exxon Valdez Oil Spill on River Otters: Injury and Recovery of a Sentinel Species

R. Terry Bowyer; Gail M. Blundell; Merav Ben-David; Stephen C. Jewett; Thomas A. Dean; Lawrence K. Duffy

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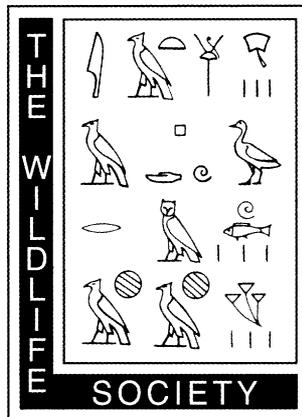
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EFFECTS OF THE *EXXON VALDEZ* OIL SPILL ON RIVER OTTERS: INJURY AND RECOVERY OF A SENTINEL SPECIES

by

R. TERRY BOWYER, GAIL M. BLUNDELL, MERAV BEN-DAVID,
STEPHEN C. JEWETT, THOMAS A. DEAN, AND LAWRENCE K. DUFFY



FRONTISPIECE. River otters are an excellent sentinel species for determining effects of pollution because of their piscivorous diet and semi-aquatic habits (photo by Andreas K. Norin).

EFFECTS OF THE *EXXON VALDEZ* OIL SPILL ON RIVER OTTERS: INJURY AND RECOVERY OF A SENTINEL SPECIES

R. TERRY BOWYER¹

Institute of Arctic Biology, and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775-7000

GAIL M. BLUNDELL²

Institute of Arctic Biology, Alaska Cooperative Fish and Wildlife Research Unit, and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775-7000

MERAV BEN-DAVID

Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, and Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-7000

STEPHEN C. JEWETT

Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775-7220

THOMAS A. DEAN

Coastal Resources Associates, Inc., 1185 Park Center Drive, Suite A, Vista, CA 92083

LAWRENCE K. DUFFY

Institute of Arctic Biology, and Department of Chemistry and Biochemistry, University of Alaska Fairbanks, Fairbanks, AK 99775-7000

Abstract: Integration of individual-based and population-level studies is essential to understanding effects of pollution on populations and ecosystems. Here we provide an example of such integration from our exploration of effects of the *Exxon Valdez* oil spill (EVOS) on river otters (*Lontra canadensis*) inhabiting the terrestrial-marine interface in Prince William Sound, Alaska, USA. Our research was divided into 2 phases: an early phase (1989–92) immediately following the oil spill; and a late phase (1996–99), which focused on potential chronic effects of oil contamination in the Sound. We used a variety of measurements that considered the physiological status and health of individual river otters, as well as aspects of their ecology, behavior, and demography. We then conducted meta-analysis to explore interactions between individual-based and population-level data in demonstrating injury and subsequent recovery of otters from ill effects of EVOS. During both phases of our studies, we first conducted intensive research at 2 study sites, which we believed to be oiled and nonoiled, and then expanded our investigations throughout similar areas of Prince William Sound. Nonetheless, our data are best interpreted as differences between heavily oiled areas and lightly oiled sites because later information indicated that our reference sites were lightly oiled. Thus we refer to heavily oiled sites as oiled and lightly oiled sites as "nonoiled." In the later phase, we were part of a broader ecosystem-based project (Nearshore Vertebrate Predators) designed to assess long-term effects of EVOS on a suite of key organisms, and to determine whether those species had recovered from that catastrophic accident.

We used radiotelemetry to locate carcasses of animals that died from natural causes, and documented that searching beaches immediately following the spill was not a reliable method for locating dead river otters. Our early research (1989–92) demonstrated that river otters living in oiled areas had lower body mass ($P < 0.04$) and elevated biomarkers ($P < 0.05$) in their blood (e.g., haptoglobin [Hp], interleukin-6 immunoreactive [IL-6 *ir*], aspartate aminotransferase [AST]) than otters inhabiting "nonoiled" areas. Likewise, otters from oiled areas had higher levels of fecal porphyrins ($P < 0.001$), ate a less-diverse diet ($P < 0.001$), had larger home ranges ($P < 0.05$), and selected habitats differently ($P < 0.01$) than otters living in areas that were not heavily oiled. A mark–recapture analysis based on radiotracers in otter feces during 1990 indicated no difference ($P > 0.10$) between density of otters in Herring Bay (oiled) or Esther Passage ("nonoiled"), but no prespill data were available. Likewise, by 1992, biomarkers (Hp, IL-6 *ir*, AST) did not differ ($P > 0.05$) between oiled and "nonoiled" areas.

¹ E-mail: ffrtb@uaf.edu.

² Present address: Alaska Department of Fish and Game, Douglas Island Center Building, 802 3rd Street, P.O. Box 240020, Douglas AK 99824-0020.

During the later phase of research, hydrocarbons on the pelage of river otters and the elevation of endothelial P450-1A, a biomarker sensitive to hydrocarbon exposure, indicated that river otters were exposed to oil still present in Prince William Sound. Nonetheless, body mass of otters continued to increase on oiled areas over time ($P < 0.05$), and eventually did not differ from otters living in “nonoiled” sites ($P > 0.05$). All blood biomarkers (Hp, IL-6 *ir*, AST) were markedly reduced from the early phase of our research, and no longer differed ($P > 0.10$) between oiled and “nonoiled” sites. We used principal component analysis (PCA) to determine that few differences existed in an array of blood characteristics for otters inhabiting oiled and “nonoiled” sites, and those differences that did exist likely were related to diet. Corpoporphyrin III, a key biomarker in heme synthesis, was reduced ($P = 0.008$) from post-spill collections made in 1990 in the oiled area, and no longer differed ($P > 0.05$) between oiled and “nonoiled” areas in 1996. We used stable isotope analysis to investigate differences in diet of river otters inhabiting oiled and “nonoiled” areas in 1996–97. When we controlled for otters inhabiting extensive freshwater habitats (which did not occur in our early studies), no differences in diet or the trophic level of otters were identified ($P > 0.20$) for otters living in oiled versus “nonoiled” sites. Similarly, density of marine fishes (≥ 8 cm in total length) on underwater transects did not differ ($P = 0.97$) between oiled and “nonoiled” areas, although an area by year interaction occurred ($P = 0.01$). Habitat selection by otters also was altered from the early phase; river otters on both study areas selected vegetated slopes that were not steep, and selected sites with more understory (brush) and greater exposure; selection for those characteristics was more pronounced in the oiled area. Otters on both sites avoided (use $<$ availability) gravel and small rocks. Although selected variables differed between oiled and “nonoiled” sites ($P < 0.001$), the direction of selection did not differ between areas. Moreover, tidal slope did not enter any of the models, in contrast to our early studies, indicating that differences in selection were not related to avoidance of oiled shores. Home-range size declined ($P < 0.05$) for otters living in oiled areas, and no longer differed ($P > 0.7$) from animals inhabiting “nonoiled” sites. We enumerated populations from oiled and “nonoiled” areas using a combination of live-captured individuals and DNA fingerprinting using microsatellite from otter feces at latrines. We also performed a conventional reconstruction based on age structure to calculate population size in 1997. Those methods indicated that most animals in the population were recruited following the oil spill and both methods characterized slowly ($\lambda = 1.03$ – 1.06) growing or stable population in the oiled area. Age structure of river otters in the Sound differed neither between oiled and “nonoiled” areas ($P > 0.36$), nor from a harvested population of river otters in Maine ($P > 0.49$). Finally, survivorship of river otters did not differ ($P > 0.2$) between oiled and “nonoiled” areas of Prince William Sound and was high compared with data on other otter populations in North America. Our data indicate that although river otters continued to be exposed to low levels of crude oil, effects of that exposure were no longer sufficient to cause obvious injury. We cautiously conclude that river otters have recovered from the more pernicious effects of EVOS.

Based on our experiences in this research, we provide theoretical considerations for use of biomarkers in wildlife studies and describe statistical approaches, including principal component analysis of blood variables, which may assist researchers with interpreting complicated results of multiple variables and datasets. Likewise, we describe how dose–response curves should be used in understanding population-level responses to pollutants. We hope that this monograph will provide valuable insights for other wildlife biologists on the process of integration of toxicological data with that of ecological data useful for studying effects of pollution on wildlife populations and their habitats.

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Key words: Alaska, biomarkers, body mass, demography, diet, Exxon Valdez oil spill, habitat selection, home range, hydrocarbons, *Lontra canadensis*, pollution, river otter.

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INTRODUCTION

Studies investigating factors attributable to declines in wildlife populations have resulted in a distinct dichotomy in research emphases. Wildlife and conservation biologists have concentrated on ecological phenomena such as habitat destruction and fragmentation, and reduced genetic variability (Harris 1984, Eldridge et al. 1999, Zacharias and Roff 2000). In contrast, toxicologists and veterinarians have focused on species or individual responses to environmental pollutants using biomarkers (Wilson and Hunt 1975, Broman et al. 1992, Huggett et al. 1992, Vanden Heuvel and Davis 1999). Variation in individual responses to environmental pollution, however, can have profound effects on population dynamics and stability (Lomnicki 1988). Integrating both approaches, therefore, is essential to understanding processes connecting individual-based and population-level studies of pollution. For example, sublethal and chronic effects of contaminants can result in decreased reproductive success or survivorship, both of which can lead to a decline in population densities and reductions in

genetic variability within populations (Peterson 2001, Weis et al. 2001).

Devastating effects of pollution, especially in aquatic systems, have been the focus of research for many years (Wilson and Hunt 1975, Broman et al. 1992, Huggett et al. 1992, Beckman et al. 1997). Few studies, however, have addressed potential effects of pollution in one system on processes occurring in another through changes in population dynamics of animals (Newman 1998). For instance, aquatic and terrestrial systems are intricately connected through activities of vertebrate predators in riparian zones (Naiman 1988, Ben-David et al. 1998*a*, Hilderbrand et al. 1999, Helfield and Naiman 2001). Similarly, fertilization of beach-fringe vegetation with marine-derived nitrogen by birds and mammals connects marine and terrestrial systems (Anderson and Polis 1998, Ben-David et al. 1998*a*, 1998*b*; Hilderbrand et al. 1999, Hobson et al. 1999). Thus, a decline in numbers of semi-aquatic mammals may alter interactions between ecosystems. Likewise, recovery of those animals can have profound importance for ecosystem structure and function in both aquatic and terrestrial habitats. Pollution

holds the potential to force those ecosystem processes. Accordingly, integrating individual-based and population-level responses of semi-aquatic mammals provides a model for understanding effects of pollution in one system on another.

River Otters as a Sentinel Species

Semi-aquatic mammals, especially mustelids, are ideal sentinel species. A sentinel species is sensitive to pollutants, and useful for measuring or indexing levels of environmental contamination (Prichard et al. 1997, Newman 1998). Species such as mink (*Mustela vison*), European otter (*Lutra lutra*), river otter (*Lontra canadensis*), and giant otter (*Pteronura brasiliensis*) have been the subject of numerous toxicological studies (Table 1). For example, European otters were extirpated from much of their historic distribution in Europe—that decline was strongly linked to environmental contamination (Baker et al. 1981; Kruuk 1995; Gutleb et al. 1998).

Populations of river otters inhabit freshwater systems throughout most of North America (Larivière and Walton 1998), but also occur in marine environments. Although legally not considered a marine mammal, the distribution of river otters

extends along the Pacific Coast from north of the Arctic Circle to central California, and down the Atlantic seaboard from the coast of Labrador to the Gulf of Mexico (Hall 1981, Larivière and Walton 1998). This wide distribution, with river otters feeding near the apex of the trophic pyramid (Larsen 1984, Stenson et al. 1984, Bowyer et al. 1994, Ben-David et al. 1998b), makes these predators a good sentinel species (Duffy et al. 1996, Hecker et al. 1997; Table 1). Indeed, populations of river otters in North America were reduced throughout much of their range in the eastern and midwestern United States by the early 1900s because of pollution and urbanization (Larivière and Walton 1998). Diminished levels of pollution coupled with reintroductions have expanded distributions of river otters in recent years (Erickson and McCullough 1987; Serfass et al. 1993, 1998; Larivière and Walton 1998; Johnson and Berkley 1999; Raesly 2001).

River otters are relatively long-lived (≤ 13 years in the wild; Docktor et al. 1987), reproduce at an early age (some females as yearlings but most as 2-year olds; Hamilton and Eadie 1964, Docktor et al. 1987), and neither migrate nor hibernate (Melquist and Hornocker 1983, Bowyer et al. 1995). Consequently, this mustelid may be exposed

Table 1. Published literature indicating a sensitivity of mustelids to pollutants.

Pesticides	Heavy Metals	Cesium 137	PCBs	Crude Oil
Clark et al. 1981	Wren et al 1980	Clark et al. 1981	Bleavins et al. 1980	Duffy et al. 1993, 1994a, 1994b, 1996
Halbrook et al. 1981	Clark et al. 1981	Halbrook et al. 1981	Clark et al. 1981	Williams et al. 1995
Henny et al. 1981	O'Connor and Nielson 1981		Halbrook et al. 1981	Blajeski et al. 1996
Elliott et al. 1999	Sheffy and Amant 1982		Henny et al. 1981	Ben-David et al. 2000, 2001a, 2001b, 2001c
Sample and Suter 1999	Wren 1984, 1985 Francis and Bennet 1994 Halbrook et al. 1994, 1996 Kruuk et al. 1997 Gutleb et al. 1997, 1998 Evens et al. 1998 Harding et al. 1998 Dansereau et al. 1999 Duffy et al. 2000 Ben-David et al. 2001a		Harding et al. 1999 Engelhart et al. 2001	Mazet et al. 2000, 2001 Beckett et al. 2002

year-round to localized sources of pollution and offers opportunities to study acute and chronic effects of toxins, including biomagnification of heavy metals (Duffy et al. 1998, 1999a; Ben-David et al. 2001a), and accumulation of petroleum hydrocarbons (Ben-David et al. 2000). Further, river otters have home ranges that are sufficiently large (10–45 km of shoreline; Bowyer et al. 1995; Blundell et al. 2000, 2001) to integrate effects of pollution along coastlines. Vagility of this semi-aquatic mammal makes the river otter well suited for studying effects of pollution at the scale of the nearshore ecosystem.

Finally, river otters transport nutrients between marine and terrestrial systems (Ben-David et al. 1998b). This mainly piscivorous predator acquires nutrients by foraging in the nearshore environment (Bowyer et al. 1994) and then deposits them at latrine sites that are located along the coast (Ben-David et al. 1998b). Plants growing on latrine sites used by river otters incorporate marine-derived nitrogen from otter feces, urine, and anal-gland secretions. This fertilization may have a substantial effect on community composition of the beach-fringe forest (Ben-David et al. 1998b). Consequently, variation in otter numbers or distribution caused by marine pollution holds the potential to uncouple or perturb marine-terrestrial relations. Thus, river otters may be a keystone species (Mills et al. 1993, Estes 1996, Simberloff 1998) for the land-margin ecosystem.

The *Exxon Valdez* Oil Spill

On 24 March 1989, the super tanker *Exxon Valdez* ran aground on Bligh Reef just beyond Valdez Arm in Prince William Sound, Alaska, USA. The accident spilled 39,000 metric tons of North Slope crude oil, which ultimately spread across 3,500 km of shoreline in western Prince William Sound, as well as contaminating portions of the Kodiak Island Archipelago, and Kenai and Alaska peninsulas in southwestern Alaska. Crude oil initially was concentrated in the nearshore environment (O'Clair et al. 1996), a pristine system known for its rich and abundant marine life (Dean et al. 2000a). In 1996, microbial analyses indicated that oil in sediments along contaminated shorelines in Prince William Sound still

occurred in much higher concentrations than in completely nonoiled areas (Braddock et al. 1996). Oil buried in sediments, which may be resuspended during storms and tidal action, is not subject to degradation by marine organisms and therefore remains in a form that is toxic to many vertebrates (Braddock et al. 1996). Hence, effects from the *Exxon Valdez* oil spill (EVOS) may be long term and chronic. Short et al. (1996) documented a continuous decline in oil concentrations in the Sound, indicating that buried oil became less available for biological transport to marine organisms as time progressed following the catastrophe.

Numerous marine organisms were injured as a result of EVOS (Collier et al. 1996, Laur and Haldorson 1996, Loughlin et al. 1996, Piatt and Ford 1996, Ballachey and Kloecker 1997), including coastal river otters (Duffy et al. 1993, 1994a). The degree of injury and level of recovery of these species and the marine ecosystem has been the topic of international concern since 1989.

Hypotheses and Research Design

Herein, we provide a comprehensive study of effects of EVOS on river otters. We combine individual-based and population-level approaches to gain a better understanding of effects of EVOS on this sentinel and keystone species. We also provide an integrative model useful for future studies on effects of pollution on wildlife populations and their habitats.

Remaining crude oil buried in sediments of Prince William Sound offered the opportunity to follow effects of hydrocarbon pollution on the nearshore environment through time. We hypothesized that exposure to petroleum hydrocarbons would adversely influence individuals and, consequently, populations of river otters, and that the negative effect would diminish as oil levels were reduced over time.

Our studies were initiated immediately following the spill (1989–92; i.e., early phase) to test for deleterious consequences of EVOS on river otters (Duffy et al. 1993, 1994a, 1994b, 1996; Bowyer et al. 1994, 1995; Testa et al. 1994; Blajeski et al. 1996). We later resumed our efforts to investigate chronic effects of the spill (1996–99; i.e., late phase) as well as to document the status of

recovery of river otters as a part of the Nearshore Vertebrate Predators (NVP) project. That ecosystem-based project combined studies of river otters with those of sea otters (*Enhydra lutris*), pigeon guillemots (*Cepphus columba*), and harlequin ducks (*Histrionicus histrionicus*) to test for lingering effects of the oil spill in Prince William Sound (Dean et al. 2000*a,b*; Esler et al. 2000; Monson et al. 2000; Seiser et al. 2000; Dean and Jewett 2002; Bodkin et al. 2002; Dean et al. 2002; Esler et al. 2002; Golet et al. 2002; Peterson and Holland-Bartles 2002). The central question posed by the NVP study was this: had recovery occurred, and if not, was that lack of recovery a function of direct toxicological effects of oiling, indirect effects on habitat, food or its acquisition, or lingering demographic consequences from the spill (Fig. 1)? This logical approach for understanding consequences of oil fouling on a sensitive marine vertebrate has been adopted in another fragile ecosystem (Wikelski et al. 2002). Nonetheless, those potential effects of the oil spill may not be mutually exclusive; accordingly, we tested hypotheses relative to each, as well as potential interactions between direct exposure, habitat degradation, food limitation, and demographics using a weight-of-evidence approach.

Sparse data on river otters prior to the spill necessitated a comparative design, contrasting the status of otters inhabiting oiled and "nonoiled" areas of Prince William Sound. Studying effects of oil pollution on river otters, however, was challenging because of the natural history of this semi-aquatic mustelid (Larivière and Walton 1998). The secretive nature of river otters makes them extremely difficult to observe and, therefore, estimation of population densities and gathering behavioral data are problematical. Moreover, otters are difficult to capture and especially to recapture (Serfass et al. 1993, 1996; Duffy et al. 1994*b*; Blundell et al. 1999), necessitating the use of some indirect methodologies.

Our methodologies included: 1) bio-marker responses as a measure of physiological stress (morphometrics, blood and tissue parameters), 2) assessing diet and prey availability, 3) evaluating use of landscape (habitat selection and home range), and 4) studying demographics (age structure, popula-

tion estimates, and survival). This design provided an integrative assessment of both injury and recovery when the weight of evidence from data pertaining to toxicological damage and resulting ecological phenomena were considered simultaneously.

Most data we collected shortly following the oil spill already have been published in a series of journal articles, although we have not compiled them previously into a cohesive document that examined overall consequences of EVOS on river otters. We have incorporated much of those early data in combination with information collected in the late phase of our study to test hypotheses related to the injury and potential recovery of river otters in Prince William Sound.

Acknowledgments.—This long-term study was initiated immediately following EVOS in 1989 when competing proposals from C. C. Schwartz (Alaska Department of Fish and Game—ADF&G) and R. T. Bowyer (University of Alaska Fairbanks—UAF) were combined into a collaborative effort. J. B. Faro soon replaced Schwartz as the principal investigator (PI) for ADF&G, and Bowyer was joined by L. K. Duffy (UAF) and J. W. Testa (UAF) as PIs in 1990. Laboratory procedures at UAF were performed by A. Porchet throughout the course of this study. Veterinarians W. Taylor and G. Grady assisted with surgical procedures in the early phase of our study (1989–92), and J. B. Blake and T. O'Hara offered important advice throughout our project. B. Ballachey and A. Rebar provided thoughtful discussions on blood chemistry of otters. We are indebted to students from UAF, who helped with fieldwork in the early phase of our research, including J. Kristopeit, N. Chelgren, K. Rock, E. Rock, M. Strauss, K. Wilson, S. Olsen, and K. Olsen. We also thank ADF&G biologists J. Lewis, R. Nowlin, D. McAllister, and S. Patton, and ADF&G technicians B. Porter, C. Hastings, S. Bowen, and K. Koener for their assistance and hard work. Likewise, we thank ADF&G volunteers K. Dowd and B. Weiss for their help. J. B. Browning identified prey remains in feces of otters. We thank D. Albert and M. Charpeniter for assistance with statistics and Geographic Information Systems (GIS) analyses, respectively. M. Ben-David (UAF) joined the project as a volunteer in 1991, later conducted

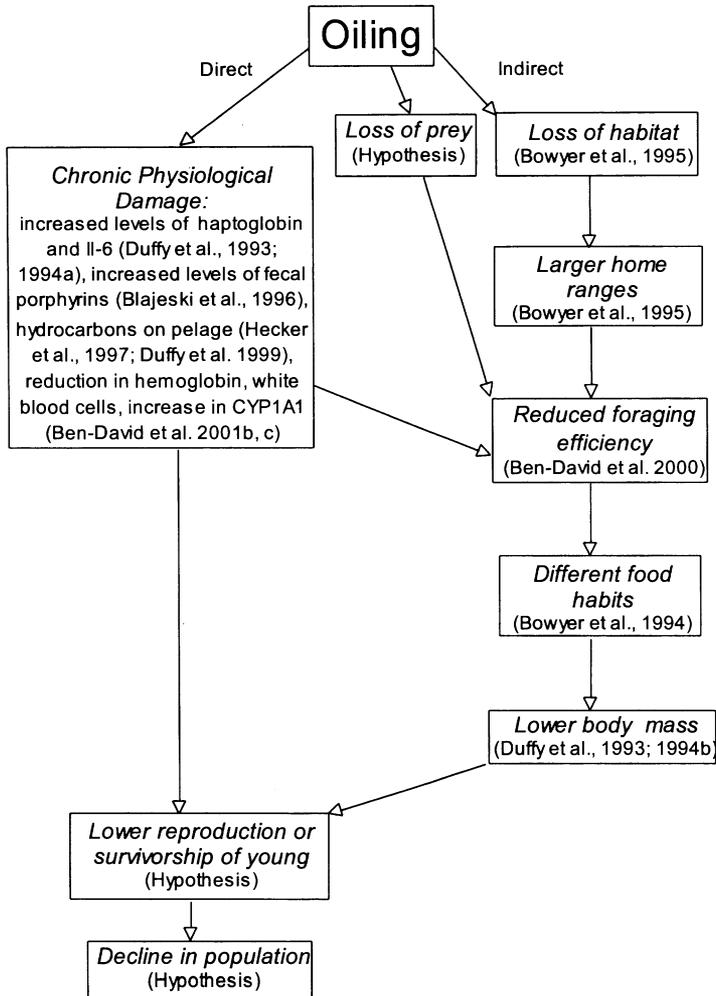


Figure 1. Potential effects of the *Exxon Valdez* oil spill on river otters in Prince William Sound, Alaska, USA.

research as a postdoctoral associate, and became a P.I. in the later phase of our research. She also conducted a companion experiment on effects of oil on captive river otters at the Alaska Sealife Center in Seward, Alaska, USA.

Findings from our earlier studies led to the listing of river otters as an injured resource by the EVOS Trustees Council in 1993; unfortunately, funding for our early research was cancelled in that same year. D. D. Roby (UAF) was largely responsible for reinitiating research in 1995, and helping to formulate ideas and write proposals that included river otters; A. D. McGuire (UAF) replaced him in 1997. G. M. Blundell (UAF) assumed responsibility for field investiga-

tions of the river otter component of the NVP project in 1996, as part of her Ph.D. research. T. A. Dean and S. C. Jewett joined the NVP project as PIs for the subtidal fish component in 1995. In the later phase of our research, we are indebted to the people of Chenega Village and the Chenega Native Corporation for permission to conduct research on their land. Radiotelemetry transmitters (implants and trap transmitters) were supplied by ADF&G, and ADF&G biologists H. Golden and D. Rosenberg provided logistical support and assistance in the field. We thank R. Colona, P. Sumner, L. Sevin, and N. Kinler for consultations regarding trapping techniques for river otters. We are indebted to students from

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mal care and use adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998).

STUDY AREA

Prince William Sound is located in south-central Alaska (Fig. 2). The area possesses a cool maritime climate and receives approximately 2,200 mm of annual precipitation and accumulates >1,000 mm of snowpack; snow often persists along shorelines until late April or early May. Dense, old-growth forest characterized by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) with a well-developed understory of *Vaccinium*, *Menziesia*, and *Rubus* is typical at lower elevations. Muskegs occasionally are interspersed with old-growth forest. Alder (*Alnus* sp.) occurs on disturbed sites near the boundary of terrestrial vegetation and the intertidal zone. Alpine tundra occurs at elevations >300 m.

In both phases of our study (early phase, 1989–92; late phase, 1996–99) we used 2 approaches: intensive studies in 1 oiled and 1 “nonoiled” area, and Sound-wide sampling of multiple oiled and “nonoiled” sites. Intensive studies conducted in 1 location for each treatment (e.g., oiled and “nonoiled”) allowed us to collect more types of data over a long period. That approach, however, created the potential for bias relative to site-specific phenomena. To overcome that problem, we employed Sound-wide surveys that provided replicate data from several sites for each treatment.

Our intensive sites of study from 1989 to 1991 were Herring Bay and surrounding areas (90 km of shoreline) on northern Knight Island (60°30'N, 147°40'W) as the oiled area, and Esther Passage (82 km of shoreline) between the mainland and Esther Island (60°53'N, 147°55'W) as our “non-oiled” site. Study areas were composed of continuous coastline and the circumference of all islands adjacent to that shore. The distance between those 2 areas is approximately 60 km. In 1991–92, Sound-wide sampling included the following oiled areas: 1) Herring Bay and Bay of Isles (60°23'N, 147°40'W) on Knight Island, 2) Eleanor Island (60°32'N, 147°37'W), 3) Naked Island (60°40'N, 147°25'W); and “nonoiled” areas:

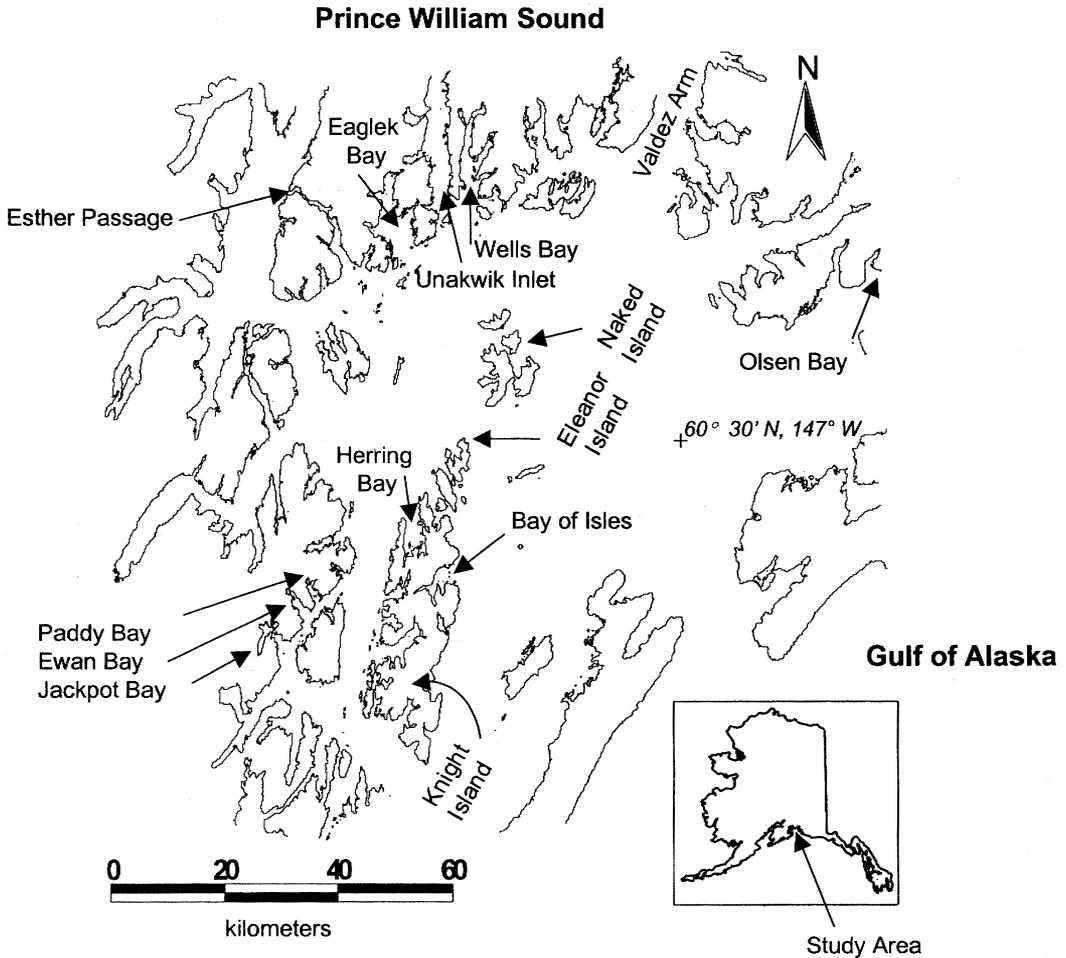


Figure 2. Areas of Prince William Sound, Alaska, USA, where river otters were live-captured from 1990 to 1998.

1) Esther Passage, 2) Eaglek Bay ($60^{\circ}52'N$, $147^{\circ}45'W$), 3) Unakwik Inlet ($60^{\circ}55'N$, $147^{\circ}30'W$), and 4) Olsen Bay and surrounding areas ($60^{\circ}44'N$, $146^{\circ}10'W$).

Because of the need to coordinate our research with other components of the NVP study, we selected a new reference site in 1996, while the oiled site remained the same throughout. We did not observe obvious signs of oil contamination in areas we considered our reference sites. Nonetheless, a LANDSAT Thematic Mapper (TM) image taken by the Geophysical Institute at UAF about 2 weeks after EVOS, but published years later (Stringer et al. 1992), clearly showed light oiling along the shorelines of our original reference area (Esther Passage). Consequently, we selected a new reference

site for the later phase of our research that, based on field observations and LANDSAT imagery, was similar in degree of oiling to our original reference site. In retrospect, we believe our data are best interpreted as differences between heavily oiled areas and lightly oiled sites. For simplicity, however, we refer to those areas as oiled and "nonoiled" throughout the monograph.

Our intensive sites in the late phase of the study (1996–99) were (oiled) Herring Bay and surrounding areas (45 km of shoreline) and ("nonoiled") Jackpot, Ewan, Paddy bays (55 km of shoreline) along Dangerous Passage ($60^{\circ}20'N$, $148^{\circ}10'W$) hereafter collectively referred to as Jackpot Bay. Study sites in 1996–97 were located approximately 30 km apart. In 1998, Sound-wide sampling

included the following oiled areas: 1) Herring Bay, 2) Eleanor Island, 3) Naked Island; and "nonoiled" areas: 1) Esther Passage, 2) Wells Bay (60°55'N, 147°20'W), and 3) Unakwik Inlet.

METHODS

Because most data we collected in the early phase of our research (1989–92) already have been published with detailed description of methods, we refer to those initial publications for methods not included herein. Here we only provide a short account of those methods to assist the reader in interpreting the associated results.

Live-capture of River Otters

In the early phase of our research from 1989 to 1992, river otters were captured with Hancock traps (Northcott and Slade 1976). All traps were placed in blind sets (i.e., no bait or lure) on trails at latrine sites and monitored by means of trap transmitters (Telonics®, Mesa, Ariz., USA) that signaled when a trap had sprung (Duffy et al. 1993). River otters were anesthetized in the trap with a hand injection of ketamine hydrochloride (22mg/kg). Otters then were transported to a 15-m boat that served as a logistical center.

River otters were captured (Blundell et al. 1999) from May through July 1996–97, and from mid-April through May 1998, with No. 11 Sleepy Creek® double-jaw leg-hold traps (Sterling Fur and Tool Co., Sterling, Ohio USA). Those traps have a center-mounted swivel located under the trap pan instead of in the customary location on 1 of the springs. We inserted additional swivels into the chain approximately every 35 cm and at the anchor point for the trap; chain length varied according to the topography of the site. Those precautions allowed the trap to swivel on the chain as the captured otter rolled, thereby avoiding serious injury to the animal (Blundell et al. 1999). Vegetation that could become tangled in the chain and prevent it from swiveling was removed from within the range of the trap. Blundell et al. (1999) provide further information concerning trapping techniques. In addition to leg-hold traps, we also used Hancock traps to capture otters in 1996 (Duffy et al. 1993,

Blundell et al. 1999). As with our early capture efforts, all traps were placed in blind sets on trails at latrine sites and monitored by means of trap transmitters. River otters captured in leg-hold traps were anesthetized with Telazol® (9 mg/kg; A. H. Robins, Richmond, Virginia, USA) administered by Telinject® (Saugus, California, USA) darts with a blowgun. Otters were processed at the capture site during the later phase of our studies, and were placed in holding boxes to recover from anesthesia. Once sufficiently recovered, river otters were able to release themselves (usually within 1–2 hr) by investigating the recovery box and pushing open a hinged door. We used leg-hold rather than Hancock traps later in our project because they were smaller and easier to transport and set, and because leg-hold traps caused less serious injury to the teeth of river otters than did Hancock traps (Blundell et al. 1999).

In the later phase of our research, we inserted a passive integrated transponder (PIT) tag under the skin between the scapulae of each new otter captured to provide a method of permanent identification. All otters captured since 1996 were electronically scanned for PIT tags to determine whether they were recaptures.

Legal harvest of river otters was closed by the Alaska Department of Fish and Game on our study areas during both early and late phases of the research. That closure prevented sport harvest of otters but not subsistence-related use. In the early phase, there was no harvest of otters in our study areas. In the later phase, however, subsistence harvest occurred in the western Sound although no otters were taken from our study sites. As a precaution to prevent the loss of our study animals, and with the cooperation of the native corporations of Prince William Sound, in particular Chenega Native Corporation, we obtained a federal subsistence closure for harvest of river otters in western Prince William Sound in 1997–98. That federal closure was the first granted for research purposes.

Surgical Procedures

Throughout our research, after morphometric measurements and biosamples were collected, a subset of captured otters that

were deemed to be in good health were implanted with radiotelemetry transmitters (Telonics®; Rock et al. 1994, Testa et al. 1994, Bowyer et al. 1995, Blundell et al. 2000). We determined health status based on pelage quality, body mass, body temperature, and the absence of severe injury or signs of illness (e.g., respiratory distress, diarrhea, or mucosal discharges). No adverse effects on reproduction have been reported for river otters implanted with intraperitoneal transmitters (Reid et al. 1986). In 1990–91, otters were implanted with transmitters in both Herring Bay and Esther Passage. In 1996, only otters captured in Jackpot Bay were implanted, whereas in 1997 otters in both Herring and Jackpot bays were implanted with transmitters. In 1998, we implanted otters captured in Herring Bay, but did not implant otters in Jackpot Bay during that year (Appendix A).

In the later phase of our research, the abdomen of each otter was palpated for potential nonfunctional transmitters that may have been implanted previously (either from 1990–92 studies in Herring Bay, or a failed transmitter from more recent studies in both areas). Only 1 previously telemetered individual was captured; that otter was released without removing or re-implanting a transmitter.

Shortly before surgery, we examined the otter to ascertain depth of anesthesia and proper analgesia. If a second dosage of anesthetic was required in 1990–91, Telazol® (11 mg/kg) was administered. In 1996–98, additional anesthesia was achieved with a combination of ketamine hydrochloride (100 mg/ml, Ketaset®, Aveco Co., Fort Dodge, Iowa, USA) at a dosage of 10 mg/kg, and midazolam hydrochloride (5 mg/ml, Versed®, Hoffman-LaRoche, Nutley, New Jersey, USA) at a dosage of 0.25 mg/kg (Spelman et al. 1993) mixed in the same syringe and administered intramuscularly. All surgeries employed sterile techniques. The site was shaved and surgically scrubbed with Nolvasan soap, alcohol, and a final iodine preparation was applied. An incision was made on the right side, posterior to the last rib to introduce a hermetically sealed radiotransmitter (IMP/400/L—Telonics®) into the peritoneal cavity. The transmitter signaled a mortality mode

if the otter remained motionless for 9 hrs. Each muscle layer was closed separately with absorbable suture material (00 Vicryl® ProVet, Seattle, Wa., USA) with simple interrupted sutures. The skin was closed with simple interrupted sutures in the early studies, but with a continuous subcuticular suture line in the later years to prevent the otters from accessing the sutures. As a final precaution, the skin incision was sealed with surgical glue. In 1990–91, otters were allowed to recover from anesthesia on the boat and released 5–13 hr after surgery near their site of capture, whereas in 1996–98 individuals were allowed to recover in a box at the capture site and released themselves once they recovered sufficiently (1–2 hr after surgery).

Morphometrics

Field Methods.—Data on morphometrics, collected from anesthetized river otters, included body mass (nearest 0.1 kg); body length, tail length, and total length (nearest 1 mm); total skull length and width of zygomatic arch (nearest 1 mm); length and diameter of canine tooth, distance between canines (nearest 0.01 mm); length from hock to toe, and interdigital spread of the right hind foot (nearest 0.1 mm). Sex was distinguished by the relative position of urogenital openings and palpation of bacula (Stephenson 1977, Chilelli et al. 1996). Females were examined for evidence of estrus and lactation. For males, bacula lengths and testicle widths were measured to the nearest 0.1 mm. Age of otters (pup, young adult, adult, and old adult) was estimated based on body size, tooth wear and staining, and in 1997 the first upper premolar was extracted for age determination with cementum annuli (Matson Laboratory, Milltown, Montana, USA).

Data Analysis.—We tested for differences in body mass between oiled and “nonoiled” areas. We performed analysis of covariance (ANCOVA) to control for effects of age and sex in river otters with body mass as the dependent variable, area as the factor, and age, sex, and total length as covariates (Zar 1999). We tested changes in adjusted mean body mass of otters living in oiled areas through time with the Spearman rank correlation (Conover 1980).

Biosampling in the Field

Rationale.—We judged that killing a sufficient number of river otters to test for differences in concentrations of hydrocarbons in tissues, and any pathological expression of that exposure, between otters from oiled and “nonoiled” areas might extirpate subpopulations or cause genetic bottlenecks; otters occurred at low densities even in “nonoiled” areas (Testa et al. 1994). Thus, we recognized the need to develop a suite of biomarkers to assess exposure to and damage from hydrocarbons in living vertebrates (Duffy et al. 1996). In early studies, our analyses included a suite of blood-serum parameters as well as haptoglobin (Hp) and interleukin-6 immunoreactive (IL-6 *ir*). Hp and IL-6 *ir* indicate increased liver activity from synthesizing acute-phase proteins in response to trauma, toxicological damage, or infection (Duffy et al. 1993, 1994a, 1994b). Additionally, we assayed porphyrins extracted from fecal samples (Blajeski et al. 1996), which are tetrapyrrolic pigments involved in biosynthesis of the heme molecule. Chemically induced changes in patterns of porphyrins have been observed in several avian species following exposure to aromatic hydrocarbons (Miranda et al. 1987). Our analyses on river otters were the start of a broader biomarker program that became central to the NVP project beginning in 1996. We employed the previous suite of blood-serum parameters (Appendix B), a complete blood count (CBC; Appendix C), and 2 additional tests to document exposure to hydrocarbons, using newly developed methodologies. We tested for the presence of hydrocarbons on the pelage of river otters with a gas chromatograph-mass spectrometer (GC-MS), and included the biomarker *P450-1A* in our analyses. Cytochrome *P450s* are a group of enzymes that metabolize a wide variety of xenobiotic compounds. *P450-1A* is induced by planar aromatic or chlorinated hydrocarbons, and thus its presence serves as a nonspecific bioindicator of hydrocarbon exposure (Woodin et al. 1997; Ben-David et al. 2001c).

Documenting Exposure to Oil.—Extensive searches of oil-contaminated shorelines were conducted in Prince William Sound immediately following EVOS. Carcasses recovered from 1989–90, which were suitable for toxicological analysis, were submitted to an

EVOS-approved laboratory for evaluation of metabolites of hydrocarbons in different tissues and bile.

To establish the presence of hydrocarbons on pelage of river otters in the latter phase (1996–97), swabs were collected from fur with a 5 × 5-cm gauze swab saturated with isopropanol for GC-MS assay. Areas of pelage we suspected to be contaminated with petroleum were swabbed for 15 sec, as well as the ventral aspect of the neck, the abdomen, a swath along each side, and 1 over the length of the back. Swabs were handled with gloved hands only. Once pelage had been sampled, the swab was completely enclosed in aluminum foil and frozen (–8°C) in a portable propane freezer for later analysis in the laboratory at UAF.

Collection of Blood.—We drew blood from the jugular vein of each otter with care taken to keep samples sterile. A portion of the sample was preserved with EDTA (purple top Vacutainer®) for complete blood counts (CBC). The remaining blood (approximately 10 ml) was collected in a red top Vacutainer® and allowed to clot; serum was removed (within 8 hr) following centrifugation at 3,000 rpm for 10 min, and frozen (–8°C) for subsequent analyses of serum chemistry. Three blood smears were made for each river otter at the time the blood was drawn. In the early phase of our studies (1989–92), blood samples collected for CBC analyses were unusable because logistics resulted in long delays between blood collection and processing in the laboratory. Therefore, from 1996 to 1998, we transported blood samples via airplane to the nearest laboratory facility (Quest Laboratories, Anchorage, Alas., USA) for analyses.

Timing of Sampling.—Because many of the biomarkers we evaluated are nonspecific responses to stress or injury, we attempted to control for the influence of sexual activity on induction of biomarkers. Most captures of otters occurred during the height of the mating season (May), along with some captures before and after that period. To control for potential bias relative to differences in capture chronology, we reversed the sampling order of our study sites between years. In 1990 and 1992, otters were captured in the “nonoiled” area during the mating

season, whereas in 1991 otters were captured in the oiled area in May. We captured otters in 1996 in the oiled area during the peak of the mating season, and in 1997 we captured otters in the "nonoiled" area in May. In 1998, all otters were captured within a 6-week period immediately prior to and during mating season, alternating oiled and "nonoiled" sites for ≤ 5 calendar nights of trapping in each area. Thus, all otters had a similar biological status with respect to mating season and area (oiled or "nonoiled") in 1998.

Skin Biopsy and Collection of Fur.—From 1996 to 1998, a 3-mm disposable skin-biopsy punch was used to obtain a tissue sample from each river otter for analysis of endothelial P450-1A. Prior to collecting the sample, we clipped hair on the medial surface of the triceps on the left front limb, and a surgical scrub was performed. The tissue specimen was preserved in 10% neutral-buffered formalin immediately after collection. Fur samples (under fur and guard hair) were collected in 1996–98 for diet analysis with stable isotope ratios (Ben-David et al. 1998b).

Collection of Feces.—Feces of river otters, deposited during winter prior to the oil spill were collected immediately post-spill (1989), providing rare data on diets of river otters in Prince William Sound prior to EVOS. We collected additional feces for analyses of otter diets in summer 1989–90 (Bowyer et al. 1994). For those analyses, the latrine site was considered the sampling unit and all feces collected on a sampling occasion were stored in 1 bag. Feces collected in 1990 and 1996 and used for porphyrin analyses (Blajeski et al. 1996, Taylor et al. 2000a) were stored individually. All feces were frozen (-70°C) until analysis.

Laboratory Procedures for Biomarker Assays

GC-MS Assays.—Swab samples collected to detect the presence of hydrocarbons on pelage of river otters were extracted into isopropanol, and that extract was analyzed by gas chromatography with mass spectrometry detection (GC-MS). Mass-spectral data were acquired with selected ions for each of the hydrocarbons (phenanthrene, chrysene, petacosane, and hexacosane). The GC-MS was calibrated by injection of a standard at 6

concentrations reaching 5mg/g (ppm). Sample concentrations for each hydrocarbon were calculated from the area under the curve generated by the mass spectrometer (Duffy et al. 1999b).

Profiles of Whole Blood and Serum Chemistry.—Serum-chemistry profiles (Appendix B) were assayed with an Olympus 7000 analyzer (Olympus, Melville, New York, USA) and complete blood counts (Appendix C) were performed with a Stack-S whole-blood analyzer (Coulter, Miami, Florida, USA). Samples were analyzed at Quest Laboratories (Anchorage, Alaska, USA).

Haptoglobin.—Haptoglobins (Hp) are serum-plasma proteins that bind free hemoglobin (Hb). In the laboratory at UAF, a standard Hp assay, which used electrophoresis to separate the Hp-Hb complex from free Hb, was used to quantify the complex with densitometry (Duffy et al. 1994a, b). Results were expressed as mg Hb-bound/100 ml serum.

Interleukin 6 immunoreactive.—Levels of IL-6 *ir* were determined at UAF with an immunochemical assay. Replicates of each sample were added to a microtiter plate coated with a monoclonal antibody for IL-6. After washing away any unbound proteins, an enzyme-linked polyclonal antibody for IL-6 was added to the wells and incubated to allow for binding. After a final wash, a substrate solution was added to the wells. Following color development, sample concentrations were determined from a standard curve (Duffy et al. 1994a, b).

Cytochrome P450-1A.—The induction of cytochrome P450-1A (CYP1A) in endothelial tissues of river otters was evaluated by immunohistochemistry. Tissue samples were analyzed at the Woods Hole Oceanographic Institute (Woods Hole, Massachusetts, USA), in the laboratory of J. J. Stegeman. To assay P450-1A activity, tissue samples were prepared, embedded, sectioned, stained, and scored for staining intensity by the same technician using procedures described in Woodin et al. (1997) and Ben-David et al. (2001c). The intensity score was multiplied by the occurrence of staining and reported as a staining index. A higher number for the index indicates a greater response in the individual to exposure to

petroleum hydrocarbons (Ben-David et al. 2001c).

Fecal Porphyrins.—The protocol used for extraction of fecal porphyrins was modified from Lockwood et al. (1985) for the earlier studies, and from Bowers et al. (1992) for the later period. Fecal extractions were measured with a Perkins-Elmer diode-array spectrophotometer. The relative concentration of total porphyrins was measured against a standard porphyrin kit (Porphyrin Products, Logan, Utah, USA). The concentration of total porphyrins in each sample was calculated from the equation:

$$\text{Total Porphyrins (nmole/g dry feces)} \\ = \text{TD} \times (6/\text{stdTD}) \times 20\text{ml}/(\text{DW} \times \text{VU}),$$

where TD = trough depth of sample, measured from baselines; 6/stdTD = trough depth of standard kit (6 nmole); DW = dry weight of sample initially used for extraction; VU = volume of sample used for diode-array analysis.

In addition, we used high-performance liquid chromatography (HPLC) to determine porphyrin profiles. The gradient-solvent system for the HPLC was modified from Lim and Peters (1984) in the earlier period of study, and from Kennedy and James (1993) in the later study. Concentration of porphyrins in each fecal sample was calculated from a calibration curve (Taylor et al. 2000b, 2001).

Data Analyses.—To establish differences in levels of hydrocarbons extracted from otter pelage (GC-MS), we used a *t*-test for unequal variances (Zar 1999) to examine differences between areas. To determine differences in levels of biomarkers between oiled and “nonoiled” areas we used several different tests such as multiple response permutation procedures (MRPP; Slauson et al. 1991), Mann-Whitney tests, as well as analysis of variance (ANOVA) when appropriate (Zar 1999). We report the test used for each analysis in results. For data collected in 1991, we used logistic regression (Agresti 1990), with 26 blood values, sex, length, body mass, and age class of otters as potential dependent variables, and area as the factor, with oiled coded 0 and “nonoiled” coded 1. We repeated that analysis for data collected in 1996–98, with the model derived from the earlier analysis.

We expanded our analyses for data collected in 1996–98 to further explore the status of recovery. We first reduced the dimensionality of the data set (i.e., 28 blood characteristics) with principal components analysis (PCA). PCA is widely used to investigate complex data sets by accounting for relations between variables and condensing the information portrayed by multiple variables into single components (McGarigal et al. 2000). PCA has been used effectively in many wildlife studies and provided insights that were not possible from other multivariate and univariate examinations of data. This methodology is used most often in studies of morphology (Bowyer et al. 2001), but Nudds (1983) delineated the niche relationships among guilds of waterfowl (Anatidae), and Kie and Bowyer (1999) evaluated the dietary niche of white-tailed deer (*Odocoileus virginianus*) using PCA.

We used the correlation rather than covariance matrix to correct for different scales of measurement among blood variables (Johnson and Wichern, 1982). We then compared 95% confidence ellipses for otters living in oiled versus “nonoiled” areas for the first 3 principle components (PCs), separated by year. By using this approach, we were able to control for the different sampling designs between years as well as to document changes through time between oiled and “nonoiled” areas. For each PC, we used those variables (blood parameters) with strong positive or negative loadings of eigenvectors to interpret the physiological significance of that PC; variables with loadings near zero contributed little to separation on a particular axis (Johnson and Wichern 1982). We followed PCA with multivariate analysis of variance (MANOVA) on untransformed data for those variables with influential loadings as dependent variables, and area and year as main effects. If MANOVA is performed on the loadings, PCA must be developed from the variance-covariance matrix, which yields biased results when original data vary markedly in scale (a common occurrence in blood values). Therefore we used a correlation matrix for PCA followed by MANOVA on original data.

If oil persisted in the environment and otters were chronically exposed, we predicted a negative relation between haptoglobin

or P450-1A and adjusted body mass of otters (from ANCOVA). Therefore, we investigated those relations using linear regression (Zar 1999) of our data collected from 1996 to 1998.

In the initial porphyrin analyses (Blajeski et al. 1996), we used the 2-sample *t*-test to compare total porphyrins in feces of river otter (Zar 1999). A 2-sample *z*-test for proportions (Remington and Schork 1970) was used to compare selected porphyrins detected by HPLC. In later analyses (Taylor et al. 2000a), we used 2-way ANOVA on ranked data, with year and area as main effects, and coproporphyrin III as the dependent variable.

Diet Analyses

Prey Remains in Feces.—Fecal samples containing primarily skeletal remains of fish and invertebrates, fish otoliths and scales, avian feathers, and mammalian hair were collected from latrine sites in our study areas in 1989–90. Samples were washed to remove soft material, air dried, and analyzed to identify prey remains. Those remains were compared with reference specimens and identified, when possible, to the species level. Keys to otoliths, scales, feathers, and mammal hair also were used for identification (Bowyer et al. 1983, 1994).

Stable Isotope Analysis.—We used stable isotope ratios to index diets of otters (Ben-David et al. 1997a, 1997b, 1998b). The specific combination of values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ result from the dietary interaction of species or individuals (Hobson 1999). Applying this technique to tissues such as blood and hair allows repeated sampling of known individuals throughout the year (Ben-David et al. 1997a, 1997b) and evaluation of changes in diet of the same individuals under differing circumstances. Stable isotope ratios of intertidal, pelagic, and freshwater fishes differ from each other (Ben-David et al. 1998b; Blundell et al. 2002). Similarly, stable isotope ratios of marine invertebrates differ from those of intertidal fishes (Ben-David et al. 1997b, 1998b). Although this technique may not identify individual species of prey, a difference in isotopic signatures in otter hair would reflect consumption of different foods (i.e., intertidal, pelagic, and freshwater fishes, and invertebrates—Ben-David et al., 1998b, Ben-David and Schell 2001).

Hair samples collected from river otters in 1996–98 were dried at 60–70°C for 48 hr. Subsequently, a subsample (1–1.5 mg) was weighed in a miniature tin cup (4 × 6 mm) for later combustion. We used a Europa C/N continuous flow mass-spectrometer (at UAF) to obtain the stable isotope ratios. Each sample was analyzed in duplicate and results were accepted only if the variance between the duplicates did not exceed that of the peptone standard ($\delta^{13}\text{C}_{\text{std}} = -15.8$, $\delta^{15}\text{N}_{\text{std}} = 7.0$, CV = 0.1; Ben-David et al. 1997a, b).

Data Analyses.—For analyses of prey remains in feces, we calculated species richness and diversity using the Shannon-Wiener index (Ricklefs 1973) for oiled and “nonoiled” areas. We used MANOVA, weighted by number of feces collected at each latrine site to evaluate effects of area and year on abundance of species in diets of river otters (Bowyer et al. 1994). We employed the McNemar test for significance of change to evaluate temporal differences in species richness in otter diets (Bowyer et al. 1994).

To establish differences in diets of otters in 1996–97, we first determined that data for stable isotopes were normally distributed. We then used MANOVA with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as dependent variables, and area, year, and sex as independent variables to test for differences in diet between Jackpot and Herring bays. We used ANOVA with $\delta^{13}\text{C}$ as the dependent variable, and year and area as factors to examine interannual variation in diet for data collected from 1996 to 1998. In that analysis, we used only $\delta^{13}\text{C}$ because that parameter more clearly distinguished between prey of river otters in Prince William Sound (Blundell et al. 2002a).

Prey Availability

Field Methods.—Demersal (nearshore) fishes were sampled at 30 latrine sites used by otters in both Herring and Jackpot bays in July 1996–97, as well as at 30 random sites at each location in both years by a team of certified research divers (American Academy of Underwater Sciences, University of Alaska Scientific Diving Program). The same scientist (S. C. Jewett) trained all personnel in fish identification prior to data collection, and data collection followed a strict protocol

developed by NVP principal investigators.

Demersal fishes were counted by 2 SCUBA divers at each site along 2 transects oriented perpendicular to shore. Transects extended 30 m, or in instances where the tidal zone was steep, until a depth of 15 m was reached. The 2 transects at each site were separated by 20 m, and originated 10 m to either side of the center of a particular site. Fishes in the water column were enumerated over a 2-m-wide swath by the first diver. Demersal fishes were counted along a 1-m-wide swath on each transect by the second diver while gently moving aside algae and other vegetation. All fishes counted were classified into 3 size classes (<8 cm, 8–15 cm, >15 cm total length) and were assigned to 8 categories: peciformes—ronquils (Bathymasteridae), pricklebacks (Stichaeidae), and gunnels (Pholididae); as well as families in other orders, including cod (Gadidae), rockfish (Scorpaenidae), sculpin (Cottidae), greenling (Hexagrammidae), and other. Fishes <8 cm were not considered because otters seldom consume fishes that small (Kruuk 1995).

Data Analysis.—To determine differences in densities of total fishes (≥ 8 cm in length) between areas and years, we employed a 2-way fixed-effects ANOVA (Zar 1999) on log-transformed data (e.g., log density + 0.1) with areas (oiled vs. “nonoiled”) and site (latrine vs. random) as main effects. Gadidae, which constitute <11% of the diet of river otters (Bowyer et al. 1994), were excluded from analyses because their behavior resulted in overestimation of their numbers; those fish tended to follow divers. Fish densities recorded at latrine and random sites were compared for Jackpot and Herring bays in 1996–97. Sample sizes were too small to permit additional analysis with families of fishes as dependent variables.

Habitat Selection

Field Methods.—Habitat selection by river otters and other mustelids can be determined by comparing habitat features at latrines and random sites, including terrestrial and marine features (Dubuc et al. 1990, Bowyer et al., 1995, Ben-David et al. 1996, Swimley and Serfass, 1998, Macdonald and Strachan 1999). Active latrine sites of river otter were identified by the presence of fresh

feces and well-established trails that were free from recent leaf litter. Each active site was characterized with respect to topography and composition of terrestrial and intertidal substrates to represent both aquatic habitats used for foraging, and terrestrial sites used for denning and social interactions (Bowyer et al. 1995, Ben-David et al. 1998b). Vegetation and intertidal substrates were assessed for a 10-m arc with its pivotal point at the mean high-tide line. We estimated relative cover of vegetation visually, with a Likert scale that ranged from 0 to 4 (Bowyer et al. 1995). We used the same method to categorize intertidal substrates. We measured vegetated slopes and tidal slopes to the nearest 5°, from the mean high-tide line to a point 10 m distant, landward and seaward, respectively, with a hand-held compass. Aspect of the site was recorded in 8 compass directions, and exposure to wave action was ranked into 3 broad categories from protected to exposed.

In 1996–97, shorelines in Herring (45 km) and Jackpot (55 km) bays were surveyed in a similar fashion to that of the early phase. Emphasis was placed on identifying active sites (>10 fresh feces) in the oiled area that were not established by river otters in 1990–91. Only new latrine sites were evaluated in Herring Bay in an effort to avoid replicating our earlier surveys. Sites that were inactive or abandoned in the later phase of the study were not included in the analysis of habitat selection for that period.

Data Analyses.—We employed step-wise logistic regression (Agresti 1990) to develop models best separating otter latrine sites (coded 1) and random sites (coded 0) for each of our study areas (oiled and “nonoiled”). Additionally, we developed a similar model for the pooled data set. We controlled for multicollinearity by eliminating 1 of any pair of variables with an absolute value of $r = 0.35$. We ensured that data did not depart from a logistic-regression model with the Hosmer-Lemeshow goodness-of-fit test. Variables that entered models were tested with a use (latrine and random sites) by area (Herring Bay and Esther Passage) MANOVA to determine whether selection differed between areas (Bowyer et al. 1995). Those analyses were conducted with data collected in both phases of our research. In

the second phase, however, we collected a subset of variables: those that distinguished between random and latrine in the early analyses. Those variables were tested with MANOVA to determine if selection still differed between oiled and “nonoiled” areas. We also developed new logistic-regression models to evaluate habitat selection in the later phase of our research.

Radiotelemetry Tracking

Field Methods.—Radiotelemetry tracking was accomplished mostly from a boat traveling along shorelines in 1990–91, as well as in 1996, because little funding was available for aerial telemetry. To minimize a possible bias from otter activities, we randomized starting times for our surveys and collected data across the full 24-hr period during summer. In the early studies, triangulations relied solely upon compass bearings, whereas in later studies a Global Positioning System (GPS) aided in triangulation. All otter positions were plotted on USGS maps (1:63360 scale).

In the early studies, otters were radio-tracked from the air once per month if individuals were not located on the study areas. All river otters were radiotracked in 1997–99 with aerial telemetry, although some supplemental radiotracking of otters in Herring Bay was conducted from a boat in 1997. Aerial tracking occurred about every 4 days from mid-April to mid-June; thereafter, tracking was conducted weekly until September. Tracking was attempted every 2–3 weeks during winter, depending upon weather. Once a telemetered otter was located from the air, GPS data were obtained for each otter by flying the plane directly over the location and recording UTM coordinates. Additionally, point locations for each otter were plotted on USGS maps (1:63360 scale). Accuracy of telemetry locations (± 30 m) was confirmed in both phases of the research by relocating transmitters placed at sites unknown to those operating receivers (Testa et al. 1994, Bowyer et al. 1995, Blundell et al. 2000).

Data Analyses.—We compared home-range size for otters inhabiting oiled and “nonoiled” areas as a method of assessing damage or recovery. In the early studies, we established the total length of shoreline

used by otters with a method developed by Bowyer et al. (1995). In that conservative method (Sauer et al. 1999), locations of otters were considered extreme values, and eliminated from the calculation of shoreline length, if an otter was located >1 km from the nearest location of that same otter. In our later studies, we calculated home-range size using a nonparametric kernel-density estimator, which defined a utilization distribution by assessing the probability that an animal would occur at particular point in space (Worton 1989, Seaman and Powell 1996). We used a fixed-kernel model (Ranges V software; Kenward and Hodddard 1996) and measured kilometers of shoreline within fixed-kernel estimates using ARC INFO (ESRI, Redlands, California, USA; Blundell et al. 2001). We excluded the few otters that moved between oiled and “nonoiled” areas from our analyses during 1996–99. We determined an adequate sample size for an individual by obtaining an asymptotic relation between home-range size and cumulative number of locations (\bar{x} = 25 locations/individual—Bowyer et al. 1995; \bar{x} = 19.5 locations/individual Blundell et al. 2001). In 1990, we relocated otters an average of 25 times per individual; in 1997–98 that value was 28 locations. We used 2-way ANOVA with area and gender as factors to test for differences in size of home ranges for otters inhabiting oiled and “nonoiled” areas from 1996 to 1999. We entered otter ID as a factor to control for multiple years of telemetry data for some individuals. As a further measure of recovery, we compared home-range data collected in 1990–92 for otters in Herring Bay with more recent (1997–99) data for otters in that same area. For continuity, we used that same methodology for home-range calculations (Bowyer et al. 1995) to compare between phases of study.

Age Structure

The status of a population can be evaluated by quantifying recruitment (i.e., number of young successfully added to the population—McCullough 1979). Because assessing reproduction in river otters is difficult, we used age structure as an indirect method of investigating differences in recruitment between oiled and “nonoiled” areas. To

determine whether that indirect measure of recruitment would be indicative of stationary or increasing populations, we also compared our data with a well-established population of river otters in Maine, USA (Docktor et al. 1987, Maine Dept. of Inland Fisheries and Wildlife Files, Orono, Maine, USA). We used a Mann-Whitney test (Zar 1999) to establish differences in age structure in populations of otters in Jackpot and Herring bays as well as between populations in Prince William Sound, Alaska, and those in Maine.

Estimating Population Numbers

Radiotracers.—In 1990, we estimated population size of river otters in oiled and “nonoiled” areas using a mark–recapture approach with radiolabeled tracers (Testa et al. 1994). Five unique tracers were used; unique combinations of several radiotracers were encased into a mold of silicone resin and implanted into the peritoneal cavity of individual otters. The implantation was considered the marking event. Samples of feces subsequently were collected from latrines and stored individually in whirlpaks and frozen for later analysis. Samples were analyzed for presence and absence of radiotracers (Testa et al. 1994 provide details) and used as recapture events. Data were analyzed with a Bayesian model to derive population estimates (Testa et al. 1994).

Microsatellite DNA.—To enumerate otter populations in Herring and Jackpot bays (Fig. 2), we used a minimum-number alive approach (Slade and Blaire 2000), based on DNA microsatellites extracted from blood and feces of river otters. Those estimates were derived from otters trapped and feces collected at latrine sites along continuous coastlines of our study areas. Consequently, our definition of populations was constrained by that sampling protocol, and does not differentiate between resident and transient animals. Nonetheless, we assume that movements of animals in and out of our designated study areas did not differ between sites. We recognized, however, that using minimum-number alive would underestimate the population (Nichols 1986), but would provide a reliable index to population density (Slade and Blair 2000).

Microsatellites are hypervariable regions of short repeats within DNA. Because

microsatellites are within noncoding regions, there is little selective pressure and those regions can change rapidly in size (Tautz 1989). With polymerase chain reaction (PCR) and specific microsatellite primers, those regions can be amplified and their sizes compared between individuals. When the appropriate suite of microsatellite markers is surveyed, a unique pattern, or fingerprint, identifying each individual arises (Crawford et al. 1991, Craighead et al. 1995). We identified individual otters from signatures of microsatellite DNA extracted from feces and blood and enumerated all unique patterns representing individuals in each area. In instances where the same DNA signature was identified in blood and feces, fecal samples were discarded.

We collected blood samples from each otter trapped in May–July 1997 in Herring and Jackpot bays. Concurrently, fresh samples of feces were collected from 42 latrine sites along the approximately 55 km of shoreline in each study area (every 4th latrine site). Similarly, DNA was extracted from blood samples of otters captured in 1996 and 1998 in those areas. Blood samples were kept frozen and fecal samples were either frozen or preserved in 100% ethanol. For live otters, DNA was extracted from white blood cells, whereas fecal DNA was extracted from intestinal cells shed within feces (Höss et al. 1992). Selected portions of DNA were amplified from small amounts of tissue with PCR (Mullis and Faloona 1987).

A library of 11 specific primers was developed for individual identification of river otters (Dallas and Piertney 1998, Fleming et al. 1999). Of those 11 primers, 9 provided complete separation of all 110 individual river otters captured in Prince William Sound from 1996 to 1998 (Blundell et al. 2002b). DNA was not successfully available for only 1 of 111 otters for which we had blood samples. A complete DNA microsatellite profile was developed for each individual and then compared with similar profiles developed for each fecal sample.

Population Reconstruction and Projections.—Populations of river otters inhabiting Herring and Jackpot bays were reconstructed based on age structure of live-captured individuals in 1997; age was determined from cementum annuli of teeth extracted

from otters. We used the conventional method of accumulating cohorts derived from capture to determine population size (Hesselton et al. 1965, Lowe 1969, McCullough 1979, Hilborn and Walters 1992, Bowyer et al. 1999, Lancia et al. 1994, Bender and Spencer 1999). This method assumes equal catchability, that survivorship and fecundity are fixed, and thereby that the population exhibits a stable-age distribution (Eberhardt 1985). Although we have no independent method to assess whether these assumptions were met, and data for other mustelids indicate changes in age distribution with resource availability (R. W. Flynn and M. Ben-David, unpublished data). Nevertheless, this technique provides a robust index to large changes in population size (Hesselton et al. 1965, Lowe 1969, Lancia et al. 1994), and can be used to compare populations inhabiting adjacent geographical areas. In addition, reconstructing populations within, rather than across years helps minimize biases associated with a stable age distribution (Bowyer et al. 1999). Moreover, such analysis provides an important independent evaluation of our conclusions regarding population status based on other methods with a weight-of-evidence approach.

To determine whether the population in Herring Bay (oiled area) declined or increased between the early and late phase of our study, we used standard methods (Caughley 1977) to calculate the intrinsic rate of increase (r) and the annual growth rate (λ) from 2 estimates. We used average population size in 1990 (Testa et al. 1994) and minimum-number alive in 1997 to calculate those parameters. Similarly, we calculated those values using data from population reconstruction based on age structure in 1997 and population estimates from 1990. To evaluate whether the rate of increase of otters in our study was at a maximum, we estimated r_{\max} for river otters by using the age structure of a population of 254 otters described by Tabor and Wright (1977), and data from Docktor et al. (1987) on *Corporea lutea* for 114 female otters to determine age-specific fecundity. We assumed a 1:1 sex ratio (Toweill and Tabor 1982). Calculations were based on the life-table approach described by Caughley (1977). Similar com-

parisons for our reference sites (Esther Passage and Jackpot Bay) would be inappropriate because of potential differences in habitat quality between areas.

Survival

In 1997–99, we used radiotelemetry to determine numbers and timing of mortality for individual otters inhabiting oiled and “nonoiled” areas. We calculated Kaplan-Meier survival estimates using a staggered-entry model described by Pollock et al. (1989). We obtained survival estimates for Herring Bay (oiled) and Jackpot Bay (“nonoiled”) and compared survivorship using the log-rank test (Pollock et al. 1989). This analysis excluded otters that traveled between study areas.

Synthesis

Data collected on river otters in both phases of the study included different variables, which may be independent from each other, and yet their combined effect provides for a weight of evidence in exploring injury and recovery. To evaluate this combined effect we used meta-analysis of combined probabilities (Sokal and Rohlf 1981). For data collected in the early phase, we used body mass, haptoglobin levels, diet, home-range size, selection of tidal slope as the variables of interest. For the later phase, we used body mass, haptoglobin levels, diet, home-range size, selection of tidal slope, age structure, and survival. We selected those variables because they provided independent measures for the status of river otters in Prince William Sound: physiological damage (e.g., body mass, and haptoglobin levels), avoidance of oil (e.g., tidal slope), and behavioral responses to damage (e.g., diet, home range size). In the later phase, we also incorporated 2 variables that represented population responses (e.g., age structure and survival). We compared results from this meta-analysis with 1 performed by Taylor et al. (2000a) on physiological responses in the early phase of the study.

RESULTS

Exposure to Oil

Carcass Counts.—The small number of river otter carcasses ($n = 12$) located along

shorelines of Prince William Sound immediately following the spill cast doubt upon how severely this mustelid might have been injured. We evaluated the utility of using carcasses of river otters as an index to mortality by examining the locations in which our radio-implanted otters perished. From 1990 to 1992, we located the carcasses of 8 otters equipped with radiotransmitters in Herring Bay and Esther Passage. Of those 8 individuals, only 2 animals died in locations where their carcasses might have been detected during beach surveys (i.e., ≤ 10 m from the shore). The remainder of mortalities was well away from the shore, or inside dens or other cavities along the beach. Even those 2 animals that did not die in cavities likely would not have been located by walking along the shore, because 1 was in an area with steep cliffs where searching on foot would have been impractical, and the other was concealed by dense vegetation.

From 1996 to 1999, we located the remains of 19 additional telemetered otters, including 10 released from the Alaska Sealife Center in 1999 (Ben-David et al. 2002). Of those animals, only 2 perished near the shoreline where those searching beaches might have detected them. Again, most otters died far away from beaches, below ground, or in deep rock crevices. The fate of those river otters would have been unknown without the aid of radiotelemetry. Indeed, during our 7 years of research, including intensive surveys of shorelines for other purposes, we encountered only 2 carcasses of unmarked river otters. Clearly, number of carcasses of river otters counted immediately following EVOS are a gross underestimate of the actual mortality; beach surveys were not a useful index to effects of that catastrophe on river otters.

Hydrocarbons in Tissues.—Of the 12 carcasses of river otters recovered from searches of oil-contaminated shorelines in Prince William Sound immediately following the spill, and 8 additional carcasses recovered from 1989 to 1990, only 2 specimens were suitable for complete toxicological analyses. Values (ppb) of phenanthrene, of 1,600 and 1,700, and naphthalene of 13,000 and 74,000 from bile indicated metabolites of hydrocarbons were present in those river otters. Analysis of lung tissue from 1 additional

otter revealed polyaromatic hydrocarbons (PAH) values of 28,000; lower PAH values for liver (455), kidney (132), and brain (311) indicated that death in that animal likely occurred prior to elevation of PAHs in tissues other than lungs. Results indicated that river otters died from acute effects of oiling, but the magnitude of that loss was uncertain because of the inability to locate mortalities and appeared small in comparison with some marine mammals killed by the oil spill (Loughlin et al. 1996).

Hydrocarbons on Otter Fur.—To establish whether river otters continued to be exposed to oil 8 years after EVOS, we used GC-MS assays to detect the presence of hydrocarbons on pelage of otters (Duffy et al. 1999b). Analyses revealed that Penta-cosane occurred significantly more often on the pelage of otters inhabiting oiled compared with “nonoiled” areas in 1997 (2 sample *t*-test with unequal variance, $P < 0.001$; Duffy et al. 1999b), but Phenanthrene and Hexacosane did not ($P > 0.05$; Duffy et al. 1999b).

Morphometrics and Biomarkers

Morphometrics.—Data on morphometrics, blood chemistry, and fecal porphyrins revealed patterns suggestive of initial physiological damage followed by subtle and potentially chronic effects from oiling. In 1990–91, river otters from oiled areas had significantly lower body mass (adjusted for length of body, sex, and age class) compared with otters inhabiting “nonoiled” areas ($P = 0.04$; Fig. 3). For example, male otters in oiled areas of Knight Island were, on average, 1.13 kg lighter than their counterparts living in “nonoiled” areas along Esther Passage from 1989 to 1990. Data from otters captured in 1992 indicated that differences in body mass between otters inhabiting oiled and “nonoiled” areas were no longer substantial (Fig. 3). Those results, however, should be interpreted with caution due to small sample sizes. Subsequent data collected from otters in 1996–98 exhibited similar convergence of body mass between oiled and “nonoiled” areas (Fig. 3). River otters in both areas gained weight in 1998, and no significant differences occurred between oiled and “nonoiled” areas ($P = 0.71$). Change in mass of otters inhabiting oiled areas

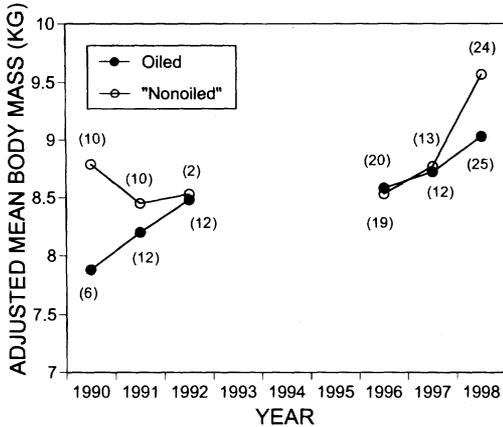


Figure 3. Mean body mass of river otters adjusted for sex, age class, and total body length with ANCOVA, inhabiting oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, following the Exxon Valdez oil spill. Sample sizes are provided in parentheses. Data are missing between 1993 and 1995. ANCOVA indicated significant differences ($P = 0.04$) between otters living in oiled and "nonoiled" areas only during 1990 and 1991. Data from 1990 to 1992 are from Duffy et al. (1993, 1994b).

consistently increased (>1 kg) with time ($\tau_3 = 1.0$, $P < 0.05$), indicating likely recovery on oiled areas.

Blood Panels.—Initial analyses of blood parameters from 1990 to 1991 revealed that mean values for haptoglobin (Hp) were elevated (MRPP, $P = 0.04$) in 8 otters from oiled areas of Knight Island (361 mg Hb-bound/100 ml) compared with 6 otters inhabiting the "nonoiled" Esther Passage (306 mg Hb-bound/100 ml; Fig. 4A). In samples collected in 1992, Hp values did not differ significantly between otters from oiled and "nonoiled" areas (Fig. 4A), but sample sizes were small (Appendix A). In 1991, IL-6 *ir* was elevated in otters from oiled sites compared with "nonoiled" sites (Fig. 4B), but in 1992, IL-6 *ir* values were below detectable levels (Duffy et al. 1994b). In 1996–98, a more sensitive assay was used permitting the detection of lower levels of IL-6 *ir* than were possible in the early years; nonetheless, no difference occurred in levels of IL-6 *ir* between oiled and "nonoiled" areas in our later studies (Fig. 4B).

Stepwise logistic regression for data collected in 1991, with 26 blood values (Table 2; Duffy et al. 1994a), sex, length, body mass, and age class of otters as potential independent variables, selected only 3 parameters.

Aspartate aminotransferase (AST), Hp, and IL-6 *ir* correctly classified 86.4% of 22 river otters as coming from oiled (coded 0) and "nonoiled" (coded 1) areas of Prince William Sound (Duffy et al. 1994a):

$$\log\left(\frac{\pi(x)}{1-\pi(x)}\right) = 5.1280 - 0.2886 \text{ Hp} \\ - 0.1043 \text{ AST} - 0.1724 \text{ IL-6 } ir.$$

Moreover, AST brought information to the model concerning other serum enzymes—AST was positively correlated with both creatine kinase (CK; $r = 0.86$) and alanine aminotransferase (ALT; $r = 0.52$). We refrained from using a similar model in 1992 because of small sample sizes.

With data collected from 1996 to 1998, we again examined levels of Hp and IL-6 *ir* in the serum of river otters inhabiting oiled and "nonoiled" areas of the Sound for comparison with earlier analyses. Values of Hp in otters captured in 1996 at previously oiled sites were higher than at "nonoiled" sites ($P = 0.01$; Fig. 4A), but no difference was detected between sites from 1997 to 1998 ($P > 0.08$). Mean levels of Hp in samples collected from 1996 to 1998 were lower than during 1990–92

Table 2. Means (\pm SE) of selected blood variables from river otters inhabiting oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, 1991 (adapted from Duffy et al. 1994a).

Blood variables	Oiled ($n = 11$)		"Nonoiled" ($n = 11$)	
	\bar{x}	SE	\bar{x}	SE
Interleukin (IL-6 <i>ir</i> , pg/ml)	48.3	13.8	17.3	11.3
Interleukin (IL-1 <i>ir</i> , pg/ml)	13.3	6.6	10.1	6.1
Haptoglobin (Hp, Hb binding d1/100 mg)	156.9	27.9	30.0	15.6
Alanine Aminotransferase (ALT, IU/L)	152.7	8.8	138.5	14.6
Aspartate Aminotransferase (AST, IU/L)	437.2	70.0	418.1	67.0
Lactate Dehydrogenase (LDH, IU/L)	146.2	25.2	154.0	43.1
Creatine Kinase (CK, IU/L)	3,038.6	820.8	1,885.8	516.4
Hemoglobin (Hb, g/dl)	16.3	0.6	15.7	0.6
Packed Cell Volume (PCV, ml/mm ³)	42.9	1.6	44.1	1.6

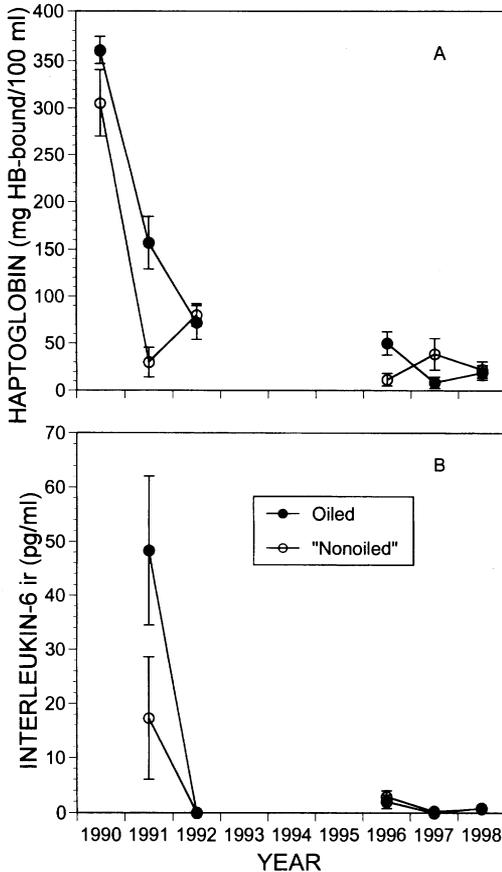


Figure 4. Mean (\pm SE) haptoglobin (A; an acute-phase protein) and interleukin-6 *ir* (B; a cytokine) values for river otters inhabiting oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, following the *Exxon Valdez* oil spill. Sample sizes are provided in Fig. 3. Data are missing between 1993 and 1995. In 1996–98 a more sensitive assay for IL-6 *ir* was used. ANOVA indicated significant differences ($P \leq 0.05$) between oiled and "nonoiled" areas in haptoglobin values in 1990, 1991, and 1996; interleukin-6 *ir* differed ($P \leq 0.05$) only in 1991.

(Fig. 4A). No differences were detected in values of IL-6 *ir* between oiled and "nonoiled" sites from 1996 to 1998 ($P > 0.05$; Fig. 4B).

In those later analyses, we attempted to model the response of river otters to exposure to oil using logistic regression and the same independent variables that were influential in classifying otters as inhabiting oiled or "nonoiled" shorelines in 1991. That identical model,

$$\log\left(\frac{\pi(x)}{1-\pi(x)}\right) = 0.5124 + 0.0010 \text{ AST} \\ - 0.0027 \text{ Hp} + 0.337 \text{ IL-6 } ir,$$

was not significant ($P > 0.13$) and classified only 58% of 112 otters correctly. Moreover, the liver enzyme AST in blood serum was elevated in otters on "nonoiled" areas in 1996–97 (Table 3), an outcome contrary to our expectations.

Endothelial *P450-1A*, an enzyme synthesized in response to exposure to hydrocarbons, was elevated in river otters captured in oiled compared with "nonoiled" areas in 1996 (Table 4), indicating continued exposure. Data on *P450-1A* collected in 1997 from those same sites, and data from 1998, which were gathered throughout western Prince William Sound, were nearly identical for otters living in oiled versus "nonoiled" areas (Table 4). Despite this apparent evidence of continued exposure as demonstrated by values of *P450-1A* from 1996, adjusted body mass as well as haptoglobin levels were indicative of recovery (Figs. 3 and 4).

Principal components analysis (PCA) on blood data from 1996 to 1998 (Tables 3 and 5) captured much of the variability (42%) in the 28 blood characteristics with 3 principle component (PC) axes. PC1 likely was created by the loading of blood parameters associated with diet (Table 6), whereas PC2 probably was indicative of general health, as identified by loadings of several liver enzymes (Table 6). PC3 likely reflected physiological responses to trapping and handling interacting with climatic conditions. When 95% confidence ellipses were plotted, illustrating the eigenvectors based on scores for individual otters relative to oiling and year, we observed a separation between years on PC1 and PC3, and a less-pronounced separation on PC2 (Fig. 5). PC1 and PC3 ostensibly reflect nutritional and physiological conditions, respectively, and are not associated with oiling, whereas PC2 probably would distinguish between areas if responses to oil were occurring (Fig. 5). In 1997, our trapping occurred during unusually warm and dry weather for the Sound. Therefore, the deprivation of food and water while an otter was in a trap probably resulted in greater physiological strain during 1997. PC3 separated 1997 from 1996 and 1998; 1996 and 1998 exhibited little separation on this axis (Fig. 5). In 1996 and 1997, PC2 distinguished between oiled and "nonoiled" areas, but liver enzymes were unexpectedly elevated in the

Table 3. Means (\pm SE) of blood-serum chemistry for river otters captured in oiled and "nonoiled" areas of Prince William Alaska, U.S.A., during 1996-98. Otters were captured in Herring Bay (oiled) and Jackpot Bay ("nonoiled") in 1996-97. During 1998, otters were live-trapped throughout oiled and "nonoiled" areas of the Sound. Abbreviations and units for blood values are provided in Appendix B.

Blood variables	1996				1997				1998			
	Oiled (n = 20)		"Nonoiled" (n = 19)		Oiled (n = 11)		"Nonoiled" (n = 11)		Oiled (n = 27)		"Nonoiled" (n = 24)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
ALB	3.01	0.05	2.91	0.06	2.92	0.07	2.96	0.07	3.05	0.05	3.09	0.05
ALK PHOS	147.85	15.04	175.53	15.43	145.09	17.11	129.36	17.11	182.22	8.68	139.79	9.21
ALT	111.00	8.96	170.05	19.85	127.82	15.20	190.0	41.51	187.81	15.78	176.88	13.68
AST	308.40	48.45	694.63	205.90	286.27	44.47	727.64	185.01	465.78	78.18	418.92	74.21
BUN	48.25	4.13	43.16	4.24	38.45	4.53	47.64	4.53	51.33	3.08	43.50	3.26
Ca	8.95	0.09	8.63	0.09	8.16	0.24	8.51	0.24	8.87	0.08	8.86	0.08
Cl	113.45	0.93	112.42	0.95	114.36	1.01	114.09	1.01	111.93	0.71	112.25	0.76
CHOL	182.40	10.90	224.05	11.18	193.64	12.28	209.36	12.28	170.81	10.29	166.04	10.91
CHOL/HDL	1.84	0.81	1.87	0.08	2.82	0.16	2.93	0.16	1.93	0.07	1.83	0.07
Dir bili	0.05	0.01	0.02	0.01	0.03	0.01	0.01	0.01	0.07	0.01	0.08	0.01
GGT	25.55	8.16	38.00	8.37	22.09	4.26	34.18	4.26	30.48	5.23	27.79	5.55
GLOB	4.40	0.12	4.67	0.12	4.42	0.16	4.77	0.16	4.16	0.09	3.83	0.10
GLU	145.45	11.11	120.26	11.40	120.00	10.96	103.64	10.96	162.74	9.56	136.79	10.14
HDL	98.70	4.61	121.58	4.73	70.00	3.45	71.64	3.45	87.56	3.56	89.13	3.78
Hp	50.08	10.01	11.77	10.27	9.53	13.47	42.22	13.47	19.30	7.81	22.38	8.28
IL-6 <i>ir</i>	2.00	1.15	2.88	1.18	0.00	0.19	0.27	0.19	0.82	0.29	0.75	0.31
LDH	200.05	43.64	319.84	44.78	174.91	63.06	346.09	63.06	187.96	25.74	221.33	27.30
LDL	71.90	7.92	89.00	8.12	112.73	9.54	124.73	9.54	72.19	6.36	65.92	6.74
PHOSPH	5.98	0.38	6.30	0.39	5.63	0.55	7.23	0.55	5.39	0.26	4.62	0.27
K	4.21	0.07	4.10	0.07	4.25	0.08	4.28	0.08	3.93	0.06	3.95	0.07
SCREAT	0.73	0.083	0.483	0.083	0.61	0.06	0.69	0.06	0.25	0.01	0.26	0.01
Na	152.15	0.82	150.89	0.84	149.55	0.69	151.45	0.69	150.00	0.60	149.50	0.63
TP	7.40	0.12	7.58	0.12	7.34	0.19	7.73	0.19	7.20	0.09	6.92	0.09
T. bili	0.28	0.02	0.32	0.02	0.31	0.01	0.32	0.01	0.30	0.01	0.33	0.01
TRIG	58.90	6.81	62.26	6.99	54.64	12.04	65.18	12.04	55.89	9.48	55.29	10.50
UA	2.81	0.26	2.36	0.26	3.16	0.43	3.46	0.43	2.24	0.19	1.83	0.20
VLDL	11.80	1.37	13.00	1.41	10.91	2.44	13.00	2.44	11.07	1.89	11.00	2.00

"nonoiled" area (Table 4); that difference disappeared in 1998 (Fig. 5). MANOVA revealed that variables contributing to separation on PC1 (Table 6) did not differ between areas ($P > 0.1$), but differed between years ($P < 0.003$). Liver enzymes influencing PC2 differed between areas ($P < 0.03$), whereas bilirubin (total and direct) and sodium did not ($P > 0.13$); ALT, direct bilirubin, and sodium were different between years ($P < 0.04$). Variables loading on PC3 (Table 7) did not differ by area ($P > 0.5$). The year effect on that axis was significant only for HDL, calcium, and serum creatinine ($P < 0.01$). Moreover, a strong year by

Table 4. Values for staining index of endothelial P450-1A (ranges from 0 to 12) for 114 river otters inhabiting oiled and "nonoiled" areas of Prince William Sound, Alaska, USA. Otters were captured in Herring Bay (oiled) and Jackpot Bay ("nonoiled") in 1996-97. During 1998, otters were live-trapped throughout oiled and "nonoiled" areas of the Sound.

Year	Area					
	Oiled			"Nonoiled"		
	n	\bar{x}	SE	n	\bar{x}	SE
1996	20	3.2	0.47	19	1.2	0.48
1997	12	4.7	0.61	12	4.0	0.61
1998	27	0.9	0.40	24	0.7	0.43
Years Pooled	59	2.4	0.38	55	1.6	0.28

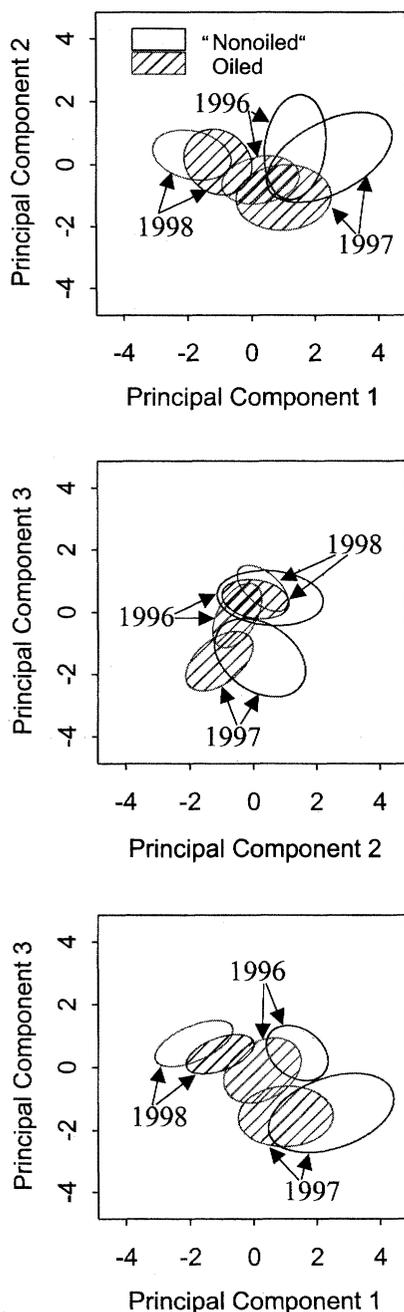


Figure 5. Principal component analysis (PCA) on blood variables of river otters captured in oiled and "nonoiled" areas in Prince William Sound, Alaska, USA, during 1996-98. Ellipses represent 95% confidence intervals for oiled and "nonoiled" areas for each year. PC1, which explained 21.1% of the variability in 28 blood values, was related to diet. PC2 (12.3%) represented the health of otters, and PC3 (9.4%) included blood values influential in explaining the response of otters to trapping conditions. Data from 1996-97 are from Herring (oiled) and Jackpot ("nonoiled") bays; in 1998 otters were captured throughout oiled and "nonoiled" areas of the Sound.

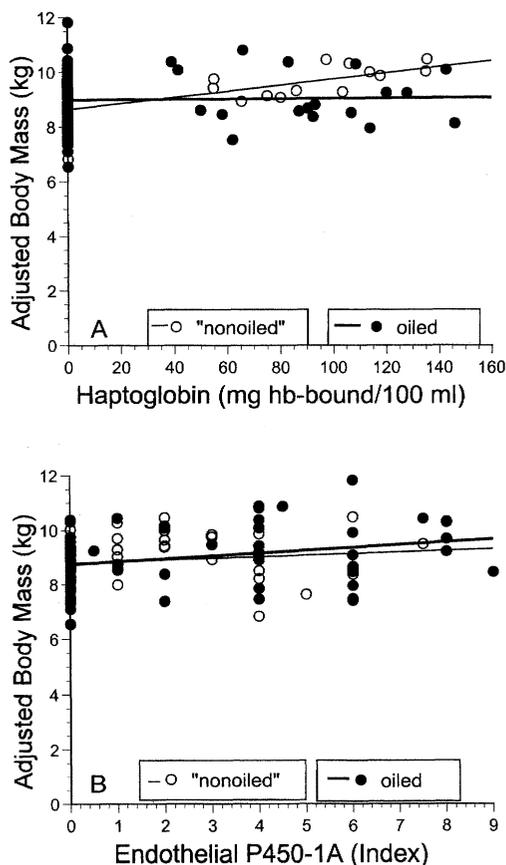


Figure 6. Linear regressions between adjusted body mass and haptoglobin (A) revealed a significant positive relation ($r^2 = 0.053$, $P = 0.014$) for all otters. When treatment were assessed individually, that positive relation was significant for otters in "nonoiled" areas ($r^2 = 0.214$, $P = 0.0004$), but not oiled areas ($r^2 = 0.007$, $P = 0.85$). The relation between adjusted body mass and P450-1A (B) exhibited a significant positive relation for all otters ($r^2 = 0.051$, $P = 0.02$), but no relation was observed in "nonoiled" areas ($r^2 = 0.014$, $P = 0.4$), and a positive relation ($r^2 = 0.083$, $P = 0.03$) was observed in the oiled area. Data were collected in Prince William Sound, Alaska, USA, from 1996 to 1998.

area interaction ($P = 0.007$) for Hp indicated PC3 did not reflect exposure to oil.

Linear regression between adjusted body mass (Table 7) and haptoglobin revealed a weak but positive relation ($r^2 = 0.053$, $P = 0.014$) for all otters (Fig. 6A). When each area (oiled or "nonoiled") was assessed individually, that relation was significant for otters in "nonoiled" areas ($r^2 = 0.214$, $P = 0.0004$) but not oiled areas (Figure 6A; $r^2 = 0.007$, $P = 0.85$). Similarly, the relation between adjusted body mass and P450-1A (Fig. 6B) exhibited a weak positive relation

Table 5. Values for complete blood counts for river otters inhabiting oiled and "nonoiled" areas of Prince William Sound Alaska, USA, during 1996–98. Otters were captured in Herring Bay (oiled) and Jackpot Bay ("nonoiled") in 1996–97. During 1998, otters were live-trapped throughout oiled and "nonoiled" areas of the Sound. Abbreviations and units for blood values are provided in Appendix C.

Blood variables	1996				1997				1998			
	Oiled (n = 20)		"Nonoiled" (n = 19)		Oiled (n = 12)		"Nonoiled" (n = 11)		Oiled (n = 23)		"Nonoiled" (n = 21)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Hct	43.07	1.36	42.09	1.36	40.23	0.96	43.10	1.00	47.18	0.84	46.98	0.92
Hgb	15.33	0.45	14.59	0.45	13.73	0.27	14.64	0.29	15.40	0.23	15.72	0.24
MCH	17.25	0.14	16.67	0.14	17.44	0.24	16.69	0.25	17.51	0.14	17.21	0.15
MCHC	35.68	0.24	34.69	0.24	34.18	0.44	34.01	0.46	33.12	0.24	33.51	0.25
RBC	8.91	0.28	8.75	0.28	7.89	0.19	8.78	0.20	8.80	0.14	9.14	0.15
RDW	33.64	1.83	31.37	1.83	19.43	2.14	26.48	2.24	28.07	1.92	31.32	2.01
WBC	11.12	1.57	11.97	1.57	10.57	1.30	14.99	1.36	11.17	1.06	10.33	1.11
Lymph	10.54	1.66	14.38	1.66	17.58	2.02	10.55	2.11	11.28	1.77	8.81	1.94
Neuts %	87.38	1.68	84.54	1.68	81.33	2.16	86.73	2.25	80.80	1.76	86.33	1.92
Mono %	1.62	0.40	0.77	0.40	0.83	0.37	1.82	0.39	5.37	0.82	4.33	0.89
Eos %	0.31	0.23	0.15	0.23	0.25	0.24	0.36	0.25	2.40	0.55	0.48	0.60
Baso %	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.05	0.03
Bands	0.15	0.13	0.15	0.13	0.00	0.24	0.55	0.25	0.00	0.03	0.05	0.03
PLAT	466.15	31.18	398.46	31.18	458.50	33.96	329.18	35.47	366.48	10.57	357.24	11.06

for all otters ($r^2 = 0.051$, $P = 0.02$), but no relation was observed in "nonoiled" areas ($r^2 = 0.014$, $P = 0.4$); a positive relation ($r^2 =$

0.083 , $P = 0.03$) occurred only in oiled areas.

Table 6. Loading values for principle component analysis (PCA) on blood values of river otters from Prince William Sound, Alaska, USA. These parameters were identified by S-Plus software as being the most influential variables in the first three principle components (PCs). The first three PCs accounted for 43% of the variability in data sets.

Variable	Loading values		
	PC1	PC2	PC3
Low Density Lipids	0.338	—	—
Cholesterol	0.335	—	—
Albumin/Globulin Ratio	-0.312	—	—
Globulin	0.302	—	—
Cholesterol/High Density Lipid Ratio	0.287	—	—
Phosphorus	0.256	—	—
Aspartate Aminotransferase (AST)	—	0.403	—
Alanine Aminotransferase (ALT)	—	0.353	—
Lactate Dehydrogenase (LDH)	—	0.293	—
Total Bilirubin	—	0.292	—
Direct Bilirubin	—	0.261	—
Sodium	—	0.255	—
Triglyceride	—	—	0.382
Very Low Density Lipids (VLDL)	—	—	0.373
High Density Lipids	—	—	0.351
Serum Creatinine	—	—	-0.302
Calcium	—	—	0.316
Haptoglobin (Hp)	—	—	-0.284

Fecal Porphyrins.—In addition to blood and tissue biomarkers, we assessed the concentration of porphyrins in feces of river otters. Porphyrins are involved in heme synthesis, a biosynthetic pathway that can be disrupted by exposure to hydrocarbons as well as other challenges (Taylor et al. 2001). Initially, we examined porphyrins in feces of river otters from oiled (Knight Island) and "nonoiled" (Esther Passage) areas in the Sound during 1990 (Blajeski et al. 1996). River otters inhabiting oiled areas exhibited higher mean (\pm SE) levels of total porphyrins in their feces (48.2 ± 2.45 nmol/g dry wt, $n = 117$) compared with animals from "nonoiled" areas (34.5 ± 3.42 nmol/g dry wt, $n = 84$; $P < 0.001$). Moreover, proportion of feces with coproporphyrins present was higher ($P < 0.05$) on oiled (26%) than "nonoiled" (11%) areas (Blajeski et al. 1996). Unfortunately, our initial analysis lacked resolution to distinguish between coproporphyrin I and coproporphyrin III. Coproporphyrin III is a critical link in the biosynthetic pathway for the synthesis of the heme molecule, whereas coproporphyrin I is not (Taylor et al. 2000b). Therefore, we repeated the porphyrin analysis specifically for coproporphyrin III (Taylor et al. 2000a).

Table 7. Body mass and total length of river otters captured in oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, 1996-98.

Sex and age classes	Oiled					"Nonoiled"				
	Body Mass (kg)			Total Length (mm)		Body Mass (kg)			Total Length (mm)	
	<i>n</i>	\bar{x}	SE	\bar{x}	SE	<i>n</i>	\bar{x}	SE	\bar{x}	SE
Males										
Yearlings	6	7.3	0.3	1218.0	30.2	6	7.3	0.6	1171.0	27.9
Adults	36	9.1	0.2	1287.0	12.2	34	9.8	0.2	1287.0	8.7
Females										
Yearlings	0	—	—	—	—	0	—	—	—	—
Adults	18	8.2	0.2	1261.0	1.7	17	8.0	0.2	1232.0	13.7

Median concentrations of coproporphyrin III in feces from Herring Bay (oiled) did not differ from those at Esther Passage ("nonoiled") in 1990 ($P = 0.09$), but a trend for elevated levels in the oiled area was detected (Fig. 7). Those levels were higher in 1990 compared with those detected in 1996 in both Herring Bay (oiled) and Jackpot Bay ("nonoiled"), which did not differ from each other (Fig. 7). The reduction in coproporphyrin III in the feces of river otters in Herring Bay from 1990 to 1996 is a strong evidence of recovery (Fig. 7).

Diet and Prey Availability

Prey Remains in Feces.—Bony fishes dominated the diet of river otters (>35%) in the

Sound during 1989–90. Those results, derived from analysis of prey remains in feces, underestimated the prevalence of bony fishes in the diet because of differential digestibility of fishes compared with other foods such as bivalves (Bowyer et al. 1994). We later confirmed this outcome with analysis of diet (80% marine fishes) based on stable isotopes (Ben-David et al. 1998b). Changes in either the species richness or diversity of otter diets were few between oiled (Knight Island) and "nonoiled" (Esther Passage) areas in winter 1989 prior to the oil spill or during the summer immediately following the contamination of shorelines with oil (Bowyer et al. 1994). By summer 1990, (>1 year after EVOS), however, substantial differences existed in the diets of otters inhabiting oiled compared with "nonoiled" areas (Bowyer et al. 1994). Moreover, changes in diets of otters in summer 1990 resulted mostly from a reduction in prey species on the oiled area (Bowyer et al. 1994). MANOVA revealed that perciform fishes (sand lances, gunnels, and ronquils) declined in diets of otters on oiled areas between pre-spill 1989 and post-spill 1990, as did archaegastropod mollusks (keyhole limpets and Margarite snails), whereas those groups increased on "nonoiled" sites during that period ($P < 0.001$). Conversely, Malacostraca (crustaceans) increased in the oiled area but declined in the "nonoiled" area (Bowyer et al. 1994).

Stable Isotope Analysis.—In 1996–97, we determined diets of river otters using stable isotope analysis of hair samples ($n = 64$). Isotopic values of otters from Jackpot Bay ("nonoiled") compared with Herring Bay

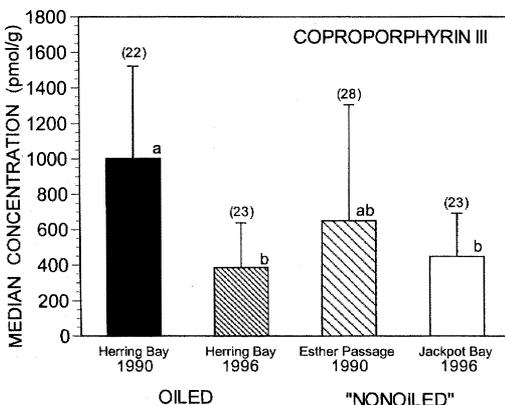


Figure 7. Median concentrations of coproporphyrin III in the feces of river otters from oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, 1 year following the *Exxon Valdez* oil spill (1990) and 6 years later (1996). Sample sizes are provided above error bars, which depict one-half the interquartile distance. Letters above bars that differ indicate significantly different ($P < 0.05$) concentrations as determined by planned contrasts from a one-tailed ANOVA on ranked data (modified from Taylor et al. 2000a).

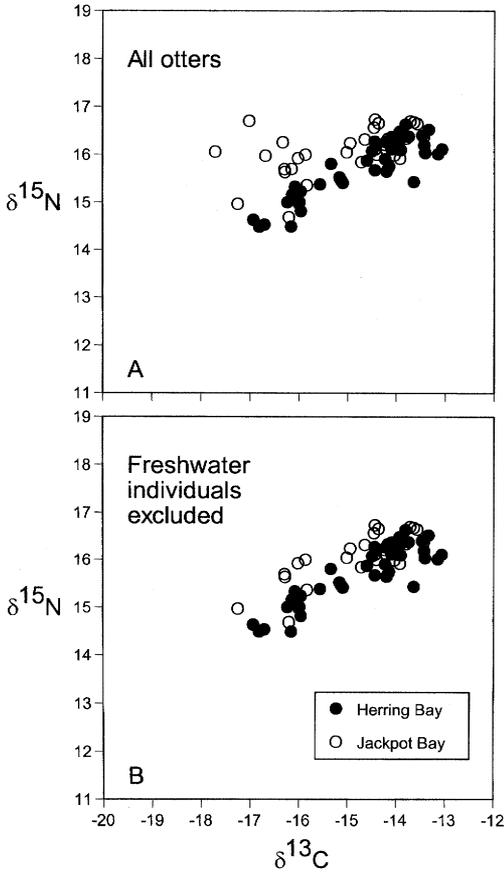


Figure 8. Stable isotope values of the guard hairs of individual river otters reflecting their diets and, hence, trophic position on oiled (Herring Bay) and “nonoiled” (Jackpot Bay) areas of Prince William Sound, Alaska, 1996–97. MANOVA with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as dependent variables with all otters ($n = 64$) included (A), produced a significant ($P = 0.02$) overall model with a year ($P = 0.001$) but no area ($P = 0.22$) effect. When 6 river otters that used fresh-water habitats (determined from radiotelemetry) were withheld from analysis (B), the overall model was no longer significant ($P = 0.20$).

(oiled) were different in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 8A; overall model, $P = 0.02$; year effect, $P = 0.001$; area effect, $P = 0.22$). That difference, however, was driven by a shift in diet for some otters in Jackpot Bay. Several individuals in that area foraged primarily on freshwater fishes. Based on telemetry locations, we excluded all otters that occurred mainly in freshwater habitats ($n = 6$) from our analysis of diet. With those otters removed, differences in diet between otters living in oiled versus “nonoiled” areas were no longer present (Fig. 8B; $P = 0.20$).

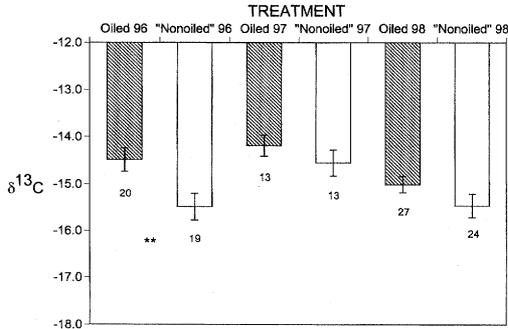


Figure 9. Values (Mean \pm SE) of $\delta^{13}\text{C}$ for river otters plotted against area and year. Sample sizes are provided below error bars. Significant differences ($P \leq 0.001$) are represented by **. Analysis revealed an area effect ($P = 0.004$), and a year effect ($P = 0.005$), but no area by year interaction ($P = 0.4$), indicating that dietary changes between years were inconsistent between oiled and “nonoiled” areas in Prince William Sound, Alaska USA, 1996–97. These differences in diet may reflect variable patterns in distribution of fishes at specific locations in different years, with no relation to EVOS..

Comparison of isotopic values relative to our earlier data from prey remains in feces should be interpreted with caution because of differences in methodologies. Nonetheless, isotopic data indicated that differences in diets of river otters no longer occurred between oiled and “nonoiled” areas in 1996–97 (Fig. 8). Stable isotope analyses ($\delta^{13}\text{C}$) for data collected from 1996 to 1998 indicated that interannual changes in diet were not consistent between areas (Fig. 9).

Prey Availability.—During the early phase of our studies, assessment of prey availability was not included in our research design because of a lack of funding. In 1996–97, however, we assessed density of marine fishes on oiled and “nonoiled” areas. In addition, we recorded the distribution of fishes relative to latrines used by river otters as well as at random sites (Table 8). Abundance of marine fishes (≥ 8 cm in total length; excluding Gadidae) sampled along underwater transects did not differ between oiled and “nonoiled” areas (Fig. 10; $P = 0.87$), or between type of site (i.e., random or latrine, $P = 0.22$). Interactions were not significant for type by area, type by year, or a 3-way interaction between those variables ($P = 0.57$, 0.65, and 0.77, respectively). Nonetheless, there was a difference between years ($P = 0.02$) as well as a year by area interaction ($P = 0.01$), indicating that annual changes in

Table 8. Densities (fish/100 m²) of marine fishes ≥ 8 cm in length at river otter latrine sites and randomly selected sites in Jackpot Bay and Herring Bay, Prince William Sound, Alaska, USA, July 1996 and 1997.

Group	1996								1997							
	Herring Bay				Jackpot Bay				Herring Bay				Jackpot Bay			
	Latrine		Random		Latrine		Random		Latrine		Random		Latrine		Random	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Greenlings	7.8	1.6	8.3	2.1	2.5	0.8	2.4	0.8	6.2	2.3	5.6	1.6	4.2	2.0	1.6	0.6
Prickle-backs	6.7	2.5	7.6	2.1	0.7	0.4	3.1	1.4	4.0	2.9	3.8	1.3	6.8	3.7	6.6	2.2
Gunnels	2.9	1.3	3.3	1.3	0.3	0.3	1.6	0.7	2.2	1.8	0.2	0.2	0.7	0.5	1.3	0.8
Cod	1.9	0.9	2.0	0.6	2.4	1.7	1.4	0.8	267.0	117.9	68.7	55.7	4.1	1.7	8.7	3.5
Rock-fishes	1.3	0.7	0.0	0.0	4.2	2.2	1.6	1.1	1.3	0.7	0.0	0.0	2.2	1.3	0.8	0.8
Sculpins	0.7	0.4	0.4	0.3	0.3	0.3	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.7	0.5
Ronquils	0.7	0.4	0.4	0.3	4.3	2.2	2.4	1.4	0.2	0.2	0.7	0.7	6.8	2.3	4.0	1.9
Others	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

prey availability were not consistent throughout Prince William Sound.

Use of Landscape

Habitat Use and Selection.—Another way in which the oil spill was expected to modify behavior and ecology of river otters was through damage to habitat. Contamination of shorelines altered use and selection of habitats by this mustelid. Because river otters concentrated their activities on and around latrines (Rock et al. 1994, Testa et al. 1994, Ben-David et al. 1998b), we compared a suite of habitat characteristics at latrines

with those at random sites along shorelines in both oiled (Knight Island) and “nonoiled” (Esther Passage) areas in 1990 (Bowler et al. 1995). We evaluated 128 latrine sites and 210 random sites in Herring Bay, and 113 latrine sites and 180 random sites in Esther Passage. Logistic regression identified 5 of 19 habitat characteristics that were influential in discrimination between used and available sites (i.e., otter latrines versus random sites), and between oiled and “nonoiled” areas (Table 9). All of those models were significant ($P < 0.001$) and between 80 and 83% of sites were classified correctly. River otters selected habitats differently between oiled and “nonoiled” areas (Fig. 11), even though availability of habitats was similar (Bowler et al. 1995; Table 9). Otters on both study areas selected (use > availability) old-growth forests, but otters inhabiting oiled areas did so more strongly; selection for brush did not differ between areas (Fig. 11; Bowyer et al. 1995). Likewise, otters on both areas avoided (use < availability) steep vegetated slopes (Fig. 11). Most notable was that otters selected steeper tidal slopes (e.g., below mean high-tide line) on oiled compared with “nonoiled” areas (Fig. 11; $P = 0.001$). We interpreted that outcome to mean that otters in the oiled area avoided shallower tidal slopes where oiling was most severe and likely persisted the longest (Bowler et al. 1995). Likewise, selection for large rocks by otters on the oiled area (Fig. 11) probably reflected an avoidance of oil accumulation on finer substrates (Bowler et

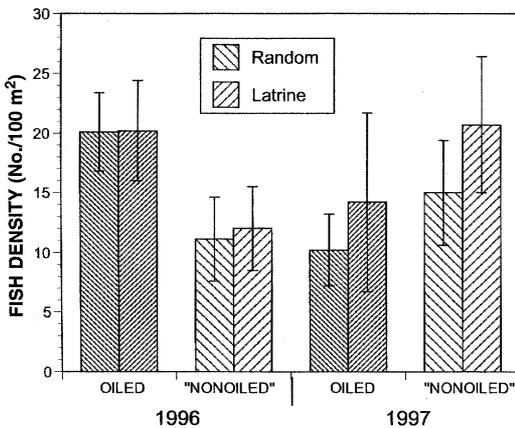


Figure 10. Mean (\pm SE) density of demersal fishes ≤ 8 cm in total length (excluding cod) sampled at both latrine sites of river otters and at randomly selected sites on oiled and “nonoiled” areas of Prince William Sound, Alaska, USA, summer 1996-97. ANOVA indicated a year effect ($P = 0.02$), and a year by area interaction ($P < 0.01$). No differences ($P > 0.05$) occurred between areas, or between latrines and random sites.

Table 9. Use (latrine sites) and availability (random sites) of selected shoreline habitats for river otters on "nonoiled" (Esther Passage) and oiled (Herring Bay) areas, during summer 1990 (adapted from Bowyer et al. 1995), and in "nonoiled" (Dangerous Pass) and oiled (Herring Bay) areas 1996–97, Prince William Sound, Alaska, USA. For 1990, only habitat characteristics that were selected from a suite of 19 variables by logistic regression are presented here; the complete list of those variables is provided by Bowyer et al. (1995).

Habitat variable	"Nonoiled" 1990				Oiled 1990				"Nonoiled" 1996-97				Oiled 1996-97			
	Random (n = 180)		Latrine (n = 113)		Random (n = 210)		Latrine (n = 128)		Random (n = 61)		Latrine (n = 89)		Random (n = 32)		Latrine (n = 67)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Tidal slope (°)	23.9	1.19	18.7	1.06	25.2	1.00	27.7	1.04	23.1	1.8	17.5	1.5	15.2	2.5	18.6	1.8
Vegetated slope (°)	37.7	1.34	26.8	1.09	36.0	1.11	29.3	0.80	46.7	2.0	29.9	1.7	36.9	2.8	31.9	2.0
Gld-growth / overstory (ranked on a 0–4 scale)	1.5	0.08	2.3	0.08	1.1	0.06	2.8	0.10	1.9	0.2	2.1	0.09	1.5	0.2	2.5	0.1
Brush / understory (ranked on a 0–4 scale)	1.4	0.07	1.0	0.07	0.6	0.05	0.5	0.05	1.9	0.1	2.1	0.09	2.3	0.2	2.9	0.1
Bedrock (ranked on a 0–4 scale)									1.3	0.2	1.9	0.2	2.0	0.3	3.1	0.2
Large rock (ranked on a 0–4 scale)	1.5	0.10	0.9	0.10	1.4	0.10	1.9	0.14	0.6	0.1	0.5	0.1	0.4	0.2	0.6	0.2
Small rock (ranked on a 0–4 scale)									0.8	0.1	0.5	0.1	0.9	0.2	0.2	0.1
Gravel (ranked on a 0–4 scale)									1.1	0.1	0.8	0.1	0.6	0.2	0.007	0.1
Sand (ranked on a 0–4 scale)									0.3	0.1	0.4	0.1	0.001	0.1	0.003	0.1
Exposure (ranked on a 1–3 scale)									1.1	0.1	1.1	0.1	0.9	0.1	1.4	0.1

al. 1995). Indeed, our initial analysis of differences in river otter use of latrines within Herring Bay immediately following the spill indicated that otters used latrine sites that were free of oil more often than latrines subjected to heavy oiling (Bowyer et al. 1995; Table 9).

In 1996–97, we evaluated 67 latrine sites and 32 random sites in Herring Bay, and 93 latrine sites and 64 random sites in Jackpot Bay. Logistic regression identified 6 of 10 habitat characteristics that were important in distinguishing between latrines and random sites (i.e., used and available), and between oiled and "nonoiled" areas (Table 9). Those models classified between 80 and

87% of sites correctly and all were significant ($P < 0.001$). River otters on both study areas selected vegetated slopes that were not steep (Fig. 11), and selected sites with more understory (brush) and greater exposure; selection for those characteristics was more pronounced in the oiled than "nonoiled" area. Otters on both sites avoided (use < availability) gravel and small rocks (Fig. 11). Old-growth forest was selected for by otters in the overall model and in the model including only habitat evaluations in the "nonoiled" area, but that variable did not enter the model for the oiled area. Although a MANOVA comparing overall differences in habitat selection between areas

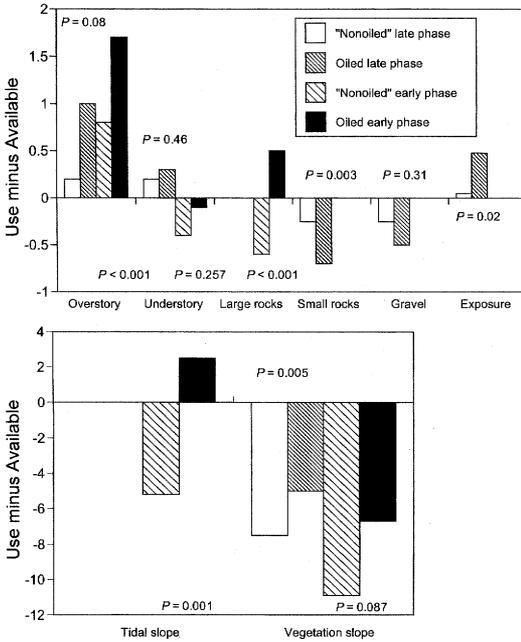


Figure 11. Used (latrine sites) minus available (random sites) shoreline habitats on "nonoiled" (Esther Passage) and oiled (Knight Island) study areas in Prince William Sound, Alaska, USA, during summer 1990 and 1996–97. Filled bars represent data from Herring Bay 1990, loose etching represents Esther Passage in 1990, tight etching represent Herring Bay in 1996–97, and clear bars represent Jackpot Bay 1996–97. Positive values indicate selection for a habitat feature, whereas negative ones represent avoidance. Analysis was conducted on untransformed data and not on the selection indices (i.e., used minus available), which are presented for descriptive purposes only. Selection of habitat variables for the MANOVA was based on results from logistic regression. P -values represent post-hoc comparisons following MANOVA. Values above bars correspond with late-phase data, whereas values below represent early phase data. Although differences in habitat selection between oiled and "nonoiled" sites still occurred in 1996–97 ($P < 0.001$), the direction of selection on oiled and "nonoiled" areas was no longer different.

was significant ($P < 0.001$), the direction of selection for all variables was similar in both areas (Fig. 11), an outcome that differed markedly from our earlier studies (Fig. 11). In addition, the variable that represented avoidance of oiled beaches (tidal slope) did not enter the model in 1996–97 ($P = 0.21$).

Home Range.—We examined home ranges (measured in kilometers of shoreline) for river otters inhabiting oiled (Knight Island) and "nonoiled" (Esther Passage) areas of Prince William Sound during summer 1990. Tracking of radiotelemetered individuals

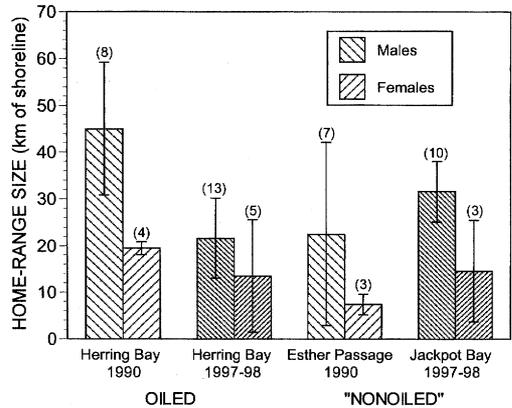


Figure 12. Home-range size ($\pm 95\%$ confidence limits) for river otters calculated with the conservative method of Bowyer et al. (1995) for oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, in 1990 and again in 1997–98. Sample sizes are provided in parentheses. A 2-way ANOVA on home-range size with area and gender as main effects on data collected in the early phase of the study indicated home ranges were larger on oiled versus "nonoiled" areas (area $P < 0.05$, sex $P < 0.1$, interaction $P > 0.75$; Bowyer et al. 1995). Note the marked decline in the size of home ranges for otters living in the oiled area (Herring Bay) between 1990 and 1997–98.

revealed that otters inhabiting oiled areas of the Sound had larger home ranges ($P < 0.05$) than those living in "nonoiled" areas (Fig. 12; Bowyer et al. 1995), indicating that otters on oiled areas needed to travel greater distances to find suitable tidal habitats.

Data from otters living in oiled (Herring Bay) and "nonoiled" (Jackpot Bay) areas collected from 1997 to 1999 indicated no difference in home-range size between areas (ANOVA, overall model, $P = 0.1$; area effect $P = 0.62$, sex effect $P = 0.02$; interaction $P = 0.69$; Fig. 12). That result held whether we used the older method developed by Bowyer et al. (1995; Fig. 12) or a probabilistic method using fixed-kernel estimates (Fig. 13). During the later phase of our study, several male river otters (11% of 37 otters) moved between oiled and "nonoiled" sites in Herring and Jackpot bays. That phenomenon did not occur in our earlier study (1990–92), ostensibly because of the long distance between Herring Bay and Esther Passage. Those individuals that moved between study sites were excluded from analyses of home range. Data from several individuals that moved between oiled and "nonoiled" areas in 1996–98 had the potential

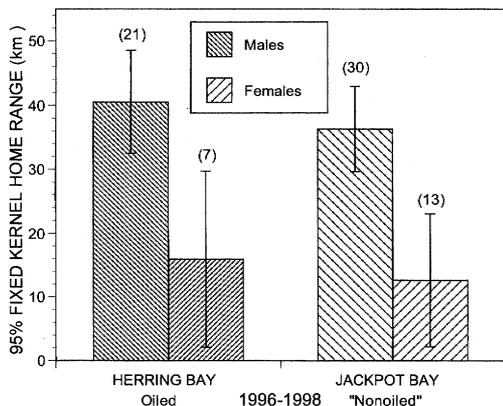


Figure 13. Mean (\pm SE) home-range size for river otters using marine habitats in Herring Bay (oiled) and Jackpot Bay ("nonoiled"), Prince William Sound, Alaska, USA, from 1996 to 1999. Ranges V software was used to calculate 95% fixed-kernel estimates of area. ARC-INFO was used to measure kilometers of shoreline within the isolines. Size of home ranges for otters in oiled and "nonoiled" areas did not differ (MANOVA blocked by otter to control for multiple years of data for the same individual; $P = 0.7$) and no differences occurred between years ($P = 0.7$). Home-range size was significantly larger for males compared with females ($P = 0.03$).

of obscuring some differences in biomarkers, and likely made that analysis conservative.

We also compared home-range size in Herring Bay in 1990 with data from 1997–99. The size of home ranges declined between study periods when compared with identical methods (Bowyer et al. 1995; Fig 12). Home-range sizes for males tended to be larger than for females in all years; differences were significant only in the more recent data (Fig. 13; $P = 0.03$).

Demography

Fecal Deposition.—River otters scent mark at latrine sites located along the coastline where this mustelid gathers to engage in social and other activities (Rock et al. 1994, Testa et al. 1994, Ben-David et al. 1998b). We used deposition of feces at latrines in 1991 to obtain a crude estimate of differences between otter populations in oiled and "nonoiled" areas (Duffy et al. 1994a). We observed that river otters inhabiting oiled areas abandoned the use of about 15% of 339 latrines, whereas otters living in "nonoiled" areas abandoned <4% of 113 latrines ($P < 0.01$; Duffy et al. 1994a). This 3-

fold difference in abandonment of latrines led us to believe that otter populations continued to decline in oiled regions compared with "nonoiled" areas.

We observed interannual and seasonal changes in use of latrine sites by otters. In 1996, new latrine sites ($n = 67$ of which 28 were active) had been established in Herring Bay and abandonment of historic sites was noted ($n = 11$ or 9%). Greater levels (>90% of 78 latrines) of abandonment of historic sites were observed in Esther Passage in August 1996. Seasonal variation in use of latrine sites was assessed by comparing fecal deposition at latrines during 2 surveys within the same year. In a survey conducted in May 1996 in Herring Bay (oiled), 41% of 121 latrine sites (including new latrines) were classified as active (≥ 10 recent feces); by August 1996, only 14% remained active. A similar pattern occurred in Jackpot Bay ("nonoiled"): 31% of 85 latrines were active in the May survey, and 5% were active in the August survey. Those data indicated that the social organization of river otters likely influenced their use of latrine sites and, consequently, interpreting such changes in the use of latrines as solely demographic could be misleading.

Population Estimates.—Population estimates for river otters inhabiting oiled areas (Herring Bay) and "nonoiled" sites (Esther Passage) were obtained by implanting otters with radiotracers and performing a mark-recapture analysis on their feces in 1990 (Testa et al. 1994). Using a Bayesian model, we obtained estimates of 36 to 42 otters/100 km of shoreline in Herring Bay and 32 to 44 otters/100 km in Esther Passage, but 95% confidence limits for the densities of river otters overlapped between oiled and "nonoiled" areas throughout summer and early autumn (Testa et al. 1994). Pre-spill estimates of otter density in Herring Bay, however, were not available (Testa et al. 1994).

In 1997, we enumerated the minimum number of river otters inhabiting oiled and "nonoiled" study sites by summing the number of unique live captures with the number of additional unique individuals identified via analysis of DNA microsatellites from feces. We developed a full microsatellite profile for a subset of those samples

(Herring Bay $n = 40$, Jackpot Bay, $n = 30$). Of those DNA profiles, one matched that of an otter trapped in 1996 in Herring Bay that was not recaptured in 1997. Two more matched the DNA profiles of animals from Jackpot Bay that were present on the study area as determined by radiotelemetry.

The minimum number of otters living in Herring Bay totaled 13 captured animals and 24 additional individuals identified from DNA in feces (37 otters/80 km), or 46 otters/100 km of shoreline. Thirteen otters were captured in Jackpot Bay ("nonoiled" site) and 8 additional otters were identified from DNA analysis (21 otters/80 km), yielding an estimated density of 26 river otters/100 km of shoreline. The minimum number of animals alive in both areas indicated that during spring 1997, river otters in Herring Bay were more numerous than in Jackpot Bay. Recaptures of individuals with either method were too few to provide reliable mark-recapture estimates.

We also reconstructed populations on both oiled and "nonoiled" areas in 1997 from captured individuals of known age using the conventional method of summing across age classes. Our point estimates, which provide a robust index, were 52 otters in Herring Bay (65 otters/100 km), and 29 otters (36 otters/100 km) in Jackpot Bay.

By comparing the population estimate of river otters obtained by Testa et al. (1994) for June 1990 in Herring Bay (42 otters/100 km) with the minimum number of otters known to be alive in that area in 1997 (46 otters/100 km), we obtain an intrinsic rate of increase, $r = 0.013 = (\ln 46 - \ln 42)/7$. Additionally, a finite growth rate of $\lambda = 1.013 (= e^{0.013})$ was obtained for that 7-year period. If we use the estimate from the reconstructed population at Herring Bay in 1997 (65 otters/100 km), $r = 0.064$ and $\lambda = 1.064$. Thus, 2 independent methods place the annual growth rate for river otters in Herring Bay (oiled area) at between 1.3 and 6.4%; we caution, however, that the enumerated value is within the 95% confidence interval calculated by Testa et al. (1994).

Age Structure.—Age structure of river otters captured in Herring Bay and Jackpot Bay exhibited few differences in 1997 (Fig. 14a). Moreover, all otters in that sample

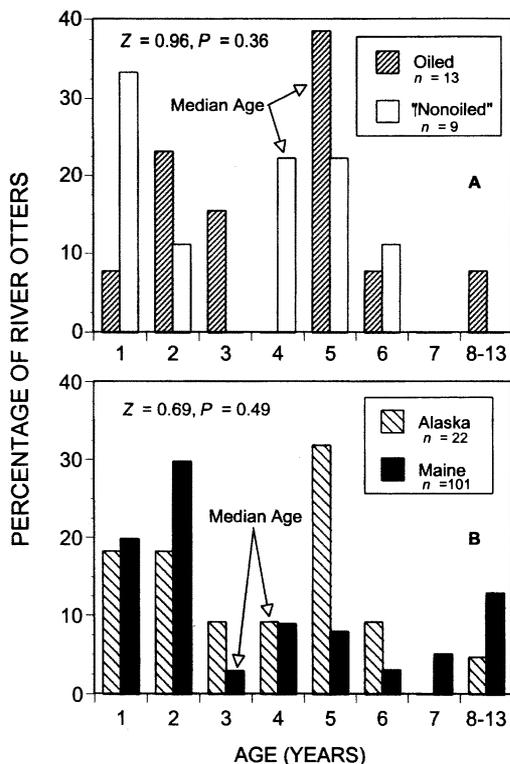


Figure 14. Age structure of river otters inhabiting oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, in 1997 (A), and a comparison of those same animals from Alaska, with river otters harvested in Maine, USA, during 1982 (B). Z-scores and P-values indicating no differences in medians were derived with the Mann-Whitney test. The zero age class was omitted because those individuals were still in dens when trapping was conducted in Alaska. Data for Alaska are from Docktor et al. (1987), and files of the Maine Department of Inland Fisheries and Wildlife.

were recruited into the population after EVOS in 1989 (i.e., the oldest individual was 8 years old). A comparison of the combined age distributions of animals from Prince William Sound (Alaska) with river otters trapped from a population in Maine, USA, revealed no significant differences (Fig. 14b). The tendency toward more middle-aged otters in Alaska, and greater numbers of younger animals in Maine may have resulted from trapping of otters in Maine for fur.

Survivorship.—Survivorship of river otters, estimated by Kaplan-Meier analyses based on radiotelemetry at one-half month intervals from late June 1997 to January 1999, did not differ between oiled and "nonoiled" areas

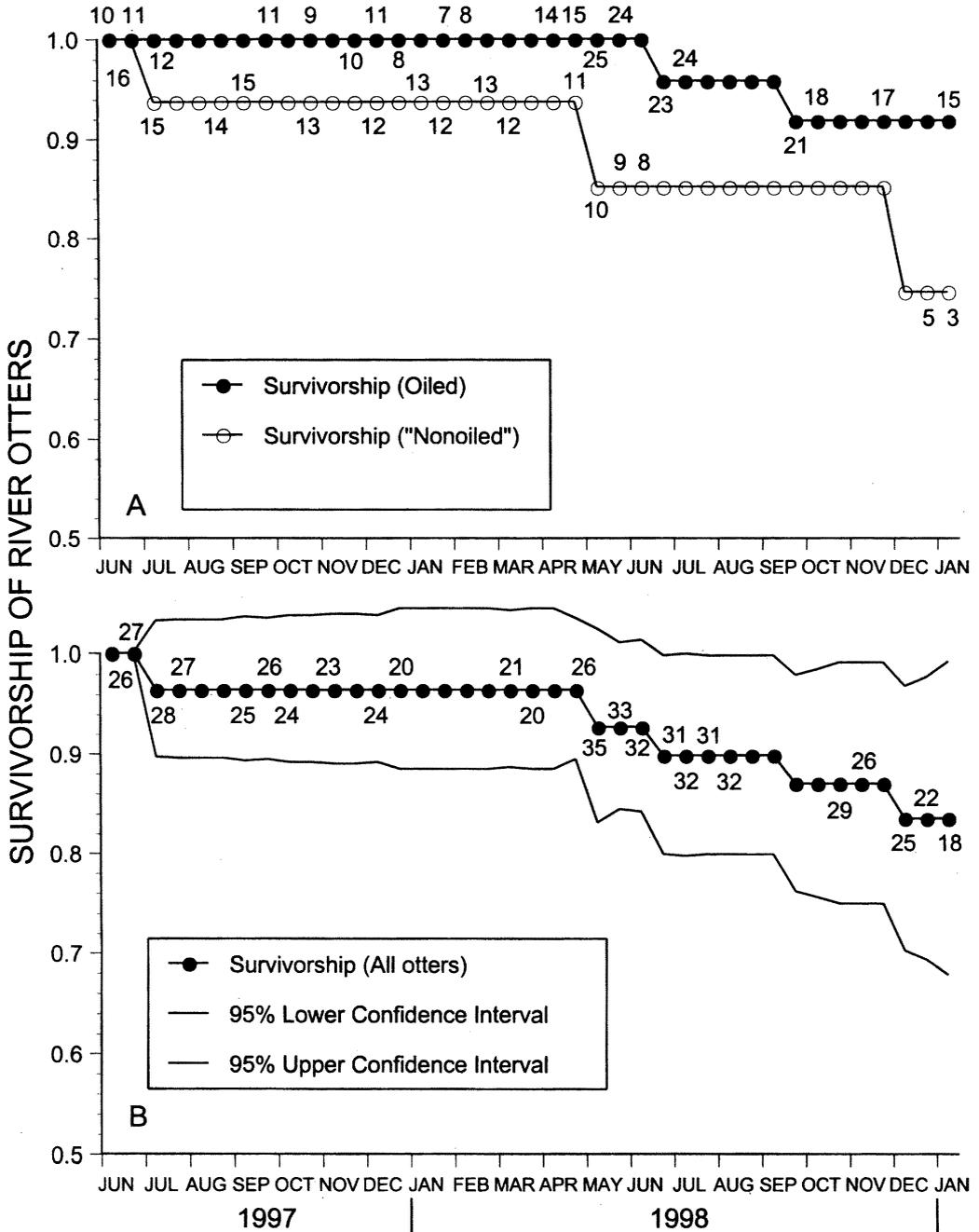


Figure 15. Survivorship of river otters with radiotransmitters inhabiting oiled and "nonoiled" areas of Prince William Sound, Alaska, USA, by one-half month intervals from late June 1997 to early January 1999 (A), and combined survivorship of otters with 95% confidence intervals for that same period (B). Numbers adjacent to circles represent changes in otters at risk used for calculating survivorship from the Kaplan-Meier, staggered-entry model (Pollock et al. 1989). The log-rank test indicated no significant difference ($P > 0.20$) in survivorship of river otters inhabiting oiled and "nonoiled" areas (A).

(Fig. 15a; $P > 0.20$). Otters on both areas were protected from sport and subsistence harvest, and overall survivorship was high (>0.8 over 20 months). Even the lower 95% confidence interval was >0.7 for that same period (Fig. 15b).

Synthesis

Meta-analysis of combined probabilities from several independent tests revealed differences between oiled and "nonoiled" areas in the early phase of the study (Table 10, $\chi^2_8 = 40.06$, $P < 0.0001$). In contrast, no such differences between oiled and "nonoiled" areas were detected in the later phase (Table 10, $\chi^2_{14} = 15.93$, $P > 0.4$). That the combined probabilities in the later phase of the study exhibited no differences between oiled and "nonoiled" areas indicates recovery from effects of EVOS.

DISCUSSION

Evaluating Injury with Carcass Counts

The initial method of determining injury immediately following EVOS was by counting the number of carcasses recovered (Dean et al. 1994, Ford et al. 1996, Piatt and Ford 1996). Our data indicated that applying that criterion to all species without considering their drastically different life-history characteristics clearly was inappropriate. River otters, which spend much of their time in terrestrial habitats and make extensive use of holes and dens (Bowyer et al. 1995), seldom died in locations where they would have been detected by those searching beaches for carcasses. The near absence ($n = 12$) of river otter carcasses recovered from the beaches of Prince William Sound was one reason this mustelid was not listed originally as an injured resource by EVOS Trustees Council, in part because of the legal need to establish the economic value of injured animals under the federal Comprehensive Environmental Resources Conservation and Liability Act (CERCLA;

Table 10. P -values for variables included in the meta-analysis of data collected on river otters in Prince William Sound, Alaska, USA, in early phase (1989–92) and late phase (1996–99).

Variable	P -value early phase	P -value later phase
Age structure	—	0.36
Body mass	0.04	0.62
Diet	0.001	0.20
Haptoglobin	0.04	0.52
Home range	0.05	0.97
Tidal slope	0.01	0.21
Survival	—	0.20

Spies et al. 1996). Integration of physiological, ecological, and behavioral data from our early studies confirmed negative effects of EVOS on river otters, which led to their recognition as an injured species in 1993. Incorporating biomarkers, diet, and landscape use, with demographics, offered a reliable approach to further assess initial injury and subsequent recovery. Our later research offered evidence that effects of EVOS on river otters had diminished; consequently, these mustelids were listed as recovered in 1999.

Exposure to Oil

Hydrocarbons were detectable immediately post-spill as indicated by high concentrations of phenanthrene and naphthalene in the tissues of carcasses recovered from beach surveys the first 2 years following the spill. Our more recent data from GC-MS analysis of pelage swabs of otters in 1997 indicated exposure to oil continued, but to a lesser degree. Concentrations of hydrocarbons on pelage of river otters (Duffy et al. 1999b) were considerably less than those reported for carcasses of sea otters collected in 1989, immediately post-spill (Ballachey and Kloecker 1997, Duffy et al. 1999b). That outcome is consistent with the decline of oil in sediments in Prince William Sound (Braddock et al. 1996, O'Clair et al. 1996, Short et al. 1996). Although tempting to do so, inferring the dosage of oil assimilated by

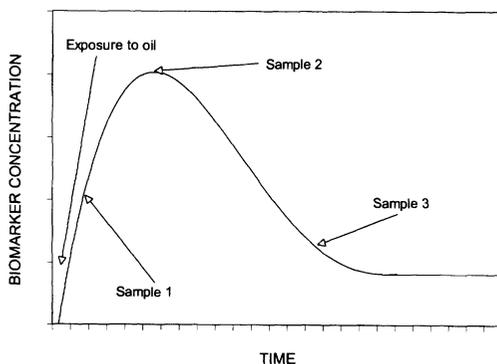


Figure 16. A hypothetical dose-response curve for concentration of a biomarker in an individual animal. Note that the time of collection of each sample (Samples 1–3) relative to the initial exposure will determine the value of the measured response. This dependency on timing of sampling renders interpretation of field data collected from a population as if it were an individual largely meaningless.

an otter based upon the concentration of oil on the pelage should not be done, because the swab might not have been wiped through the area of highest concentration on the animal. Moreover, the time of initial exposure to oil relative to the time of capture, how much oil the animal groomed from its fur, or how much oil might have been removed by otters mutually grooming are unknown (Ormseth and Ben-David 2000).

Biomarkers

Our early studies indicated elevation in levels of Hp, IL-6 *ir*, and several liver enzymes in otters living in oiled areas compared with those in "nonoiled" areas (Table 2; Duffy et al. 1993, 1994a, 1994b). By 1992, enzyme levels diminished and no differences were detected between areas. Although suggestive of recovery, those results were not conclusive because of small sample sizes, the absence of baseline data on blood chemistry of river otters in the wild (Duffy et al. 1993), the potential movements of otters between oiled and "nonoiled" areas, and the changing distribution of oil throughout the Sound (Stringer et al. 1992). The predictive model we developed with logistic regression clearly indicated differences in blood chemistry of otters inhabiting oiled and "nonoiled" areas in Prince William Sound during 1991. Nonetheless, Duffy et al. (1994a) cautioned that none of those biomarkers were specific to hydrocarbon exposure, and that elevated levels of biomarkers in river otters from oiled sites might result from interactions with other stressors associated with oiling, such as loss of body mass (Duffy et al. 1993, 1994a). Indeed, our data on adjusted body mass supported such observations (Fig. 3). Although no single result from our biomarker research from 1989 to 1992 provided an overwhelming case that river otters were damaged by EVOS, considered in concert, those results offered strong evidence that river otters were suffering subtle and chronic effects from the spill.

In our later studies, both Hp (Fig. 4a) and P450-1A (Table 4) were elevated in the oiled area in 1996 compared with the "nonoiled" area. Liver enzymes, however, exhibited the opposite trend (Table 3). Moreover, levels of Hp in both areas were substantially lower

than in previous years. This decline in Hp is further supported by our data from fecal porphyrins; elevated values in the oiled area occurred in 1990 but that difference disappeared in 1996, and overall levels were lower in the later phase (Blajeski et al. 1996, Taylor et al. 2000a). Smith and El-Far (1980) documented a relation between malnutrition and liver porphyrins. Our field data indicated a similar trend. In the early studies, otters from oiled areas had comparatively low body mass and porphyrins extracted from feces collected in those same areas were elevated (Fig. 7; Taylor et al. 2000a). Those trends disappeared in the later phase of the study, indicating recovery.

Analysis of induction of the cytochrome P450-1A enzyme offers a sensitive method to detect exposure to xenobiotics, including hydrocarbons (Woodin et al. 1997, Ben-David et al. 2001c). Although differences in P450-1A among areas may represent variation in exposure to hydrocarbons, the enzyme certainly did not evolve in river otters to help detoxify crude oil, and therefore should not be considered as responding exclusively to hydrocarbon exposure (Ben-David et al. 2001c). Much remains to be discovered about the conditions that might induce this enzyme. If levels of P450-1A, measured across differing sex and age classes of river otters, were elevated, and the primary difference was location of capture (i.e., oiled or "nonoiled"), this biomarker would provide reasonable inference of oil exposure. In 1997–98, however, no differences in Hp (Fig. 4a) or P450-1A (Table 4) were detected between oiled and "nonoiled" areas.

In our earlier studies, when values for biomarkers were high, changing timing of capture relative to mating season and area (i.e., oiled or "nonoiled") revealed no alteration in the overall pattern of biomarkers between areas. In our later studies, however, differences disappeared when otters were sampled in the "nonoiled" areas during the mating season. We hypothesize that otters in previously oiled areas were continuously exposed to low levels of oil, but significant elevation of biomarkers only occurred when additional stressors such as the mating season were added to challenges faced by those mammals. The year in which no other

notable factors (e.g., mating season or site-specific phenomena) were evident was 1998, when all samples were collected from 3 oiled ($n = 27$ otters) and 3 "nonoiled" ($n = 24$ otters) sites during the mating season. In that year, no biomarker or other index suggestive of exposure to oil or stress entered any diagnostic model, ostensibly because all otters were experiencing similar environmental conditions. Therefore, biomarkers may be informative, but caution should be used when interpreting such data. Overall weight of evidence should be used in evaluating damage or assessing risk.

Principal components analysis (PCA) clearly distinguished between years of data collected in the later phase of our research. We expected differences, a priori, in the outcomes of our analyses using a multi-year approach with pooled data, because we sampled the same 2 populations in 1996 and 1997, and different populations in 1998 (except for the inclusion of Herring Bay; 20% of the total samples for that year). Others have reported interannual variation in blood values of river otters (Tocidlowski et al. 2000). In our analysis, PC2 was characterized by liver enzymes (Table 7), a response we expected from exposure to residual oil in the environment (Duffy et al. 1993, 1994a). Separation between otters residing in oiled versus "nonoiled" areas (Fig. 5), however, was primarily because of higher values for those liver enzymes in individuals from our "nonoiled" area (Jackpot Bay) in 1996 and 1997 (Table 4). Therefore, data from 1998 are most informative in terms of recovery, because river otters were sampled from throughout western Prince William Sound, and blood values should not reflect the localized condition in Jackpot Bay or elsewhere. Moreover, timing of sampling in 1998 prevented confounding effects associated with season. In 1998, there was no difference on PC2 between oiled and "nonoiled" areas (Fig. 5). PC1, which likely reflected diets of otters, did not differ between areas, but did so between years. Those differences may reflect the distribution of fishes at various locations in Prince William Sound in different years (Table 9, Fig. 12). Indeed, Fuller and Sievert (2001) noted that changing availability of prey would be expected to alter diets of carnivores. Our conclusion is

further supported by interannual variation in diets between areas revealed by stable isotope analysis (Fig. 11). Our interpretation of why PC3 distinguished 1997 from 1996 and 1998 was the likely effects of weather on otters in traps in 1997 (an El-Niño year; Khole 2000). Other factors may be involved in loadings on PC3, but stress from weather and trapping is the most obvious explanation. Thus, we conclude that oiling played no role in differences we observed in blood parameters during the late phase of our study (Fig. 5), and that river otters probably have recovered from extreme effects of EVOS.

We expected negative relations between adjusted body mass of otters and haptoglobins or P450-1A levels if oil persisted in the environment at high levels. Linear regression of those parameters revealed no such pattern (Fig. 6). That outcome indicated that nearly a decade after the spill, either oil was absent or persisted at levels too low to cause noticeable physiological changes in river otters in western Prince William Sound. Alternatively, those particular biomarkers may not become elevated unless exposure of river otters to hydrocarbons is coupled with additional environmental challenges. Indeed, captive experiments conducted at the Alaska Sealife Center in Seward, indicated that biomarker responses of river otters to exposure to hydrocarbons in low doses were nonlinear, and opposing physiological processes co-occurred in oiled animals, which made interpretation of those biomarker data difficult (Ben-David et al. 2001b, c). No detectable relation between adjusted body mass and biomarkers in river otters in the Sound during 1998 provides additional support for our conclusion that these animals have recovered from the more pronounced effects of EVOS.

Although our results indicate recovery of river otters from effects of EVOS, we wish to alert future investigators to potential difficulties with interpretation of similar data. There is a long and successful history of interpreting blood values for domestic animals in veterinary medicine (Kerr 1989). Comparisons between captive and free-ranging animals, however, may be more difficult to make. Baseline data on the "normal" range of values for free-ranging animals seldom are available, and differences in diet,

activity, social organization (Warren and Kirkpatrick 1978, Lochmiller et al. 1986, Messier et al. 1987, Gau and Case 1999), or stress resulting from captivity (Ben-David et al. 2001*b*) can make comparisons with animals held in zoos or research facilities problematical. Likewise, capture and handling of wild mammals may affect particular blood variables (Seal et al. 1978, Boonstra et al. 1998, Keech et al. 1998). For example, values of AST, GLU, BUN, and LDH in our free-ranging otters were higher at capture than were mean values recorded for captive river otters (Davis et al. 1992, Reed-Smith 1995, Ben-David et al. 2001*b*). Values of those parameters in our free-ranging otters, however, were similar to those recorded for other wild-caught otters (Serfass et al. 1993). Until recently, traditional biomarker profiles for river otters, whether free ranging or captive, did not include many of the biomarkers we evaluated in our study (e.g., fecal porphyrins, IL-6, haptoglobin, Cytochrome P450-1A1). Lack of baseline data from free-ranging animals for those biomarkers, and the complications of effects of captivity and capture (Ben-David et al. 2001*b, c*) may lead to ambiguity in interpretation of such data.

Another difficulty related to biomarkers stems from trying to interpret data for the population as if it were an individual animal with a characteristic set of blood parameters indicative of a particular condition or disease process. Not all animals in a population would be expected to exhibit elevated blood values (or values of other biomarkers) from exposure to oil or from some other factor such as infection. Even if 50% of the population responded in the expected manner and exhibited levels that would be interpreted as clinical damage in an individual, the population mean would be much lower. Finding even a small difference in biomarkers likely has biological importance. Moreover, more than 1 toxicological or disease process might occur in the same population, which would tend to obscure the expected profile of blood parameters or other biomarkers, and make a diagnosis similar to that of an individual difficult and inappropriate.

A critical factor in interpreting blood-related data is the nature of the dose-response curve (Fig. 16). If exposure

or capture of all individuals is not simultaneous, some animals may be sampled at the peak of the biomarker response (Fig. 16, sample 2), whereas others will be sampled during the waning phase of the dose-response curve (Fig. 16, sample 3). Consequently, 2 individuals subjected to the same challenge but sampled at different stages in their response curves would have markedly different levels of biomarkers, even though both animals underwent an identical physiological process. Clearly, valid comparisons of biomarkers for free-ranging animals must be made at the population level.

Deciding which biomarkers to consider, or which blood variables should be most informative, is not simple. Including every possible blood characteristic, and sorting among the myriad of those potential variables is a daunting task, both theoretically and statistically. Our use of multivariate statistics (MANOVA, logistic regression, and principal components analysis) allowed for simultaneous consideration of nonindependent and autocorrelated variables. Our approach also reduced biases associated with analysis of extreme values (i.e., outliers; Fadely 1997). Outlier analysis may underestimate the overall population response, because that approach results in consideration only of those individuals that exhibit a peak response at sampling (Fig. 16). Nonetheless, multivariate analyses do not alleviate the need for selecting appropriate biomarkers that exhibit a specific, quantitative, predictable, dose-response relation between the contaminant and the physiological response (Vanden Heuvel and Davis 1999). Selection of such biomarkers should be consistent with models based on physiological theory (Ben-David et al. 2001*b, c*).

Diet and Prey Availability

Our earlier studies based on analyses of prey remains in feces indicated a difference in diets of river otters inhabiting oiled and "nonoiled" areas (Bowyer et al. 1994). Declines we observed in invertebrates would be expected because bivalves and limpets, which are sessile as adults, occurred in habitats that received heavy oiling (Bowyer et al. 1994). Our data on habitat selection clearly demonstrated that otters avoided oiled

shorelines in 1990 (Table 9; Fig. 11). Some changes in diets of otters may have resulted from lower prey availability in oiled areas. For example, studies of benthic communities in the Sound approximately 1 year following EVOS revealed that a suite of invertebrates, including gastropods, bivalves, and crabs, were reduced in several shallow (<20 m) subtidal habitats that were oiled (Jewett et al. 1995). Conversely, a number of demersal fishes (e.g., cod, greenling, sculpin, ronquill, and pricklebacks) were higher in abundance in shallow oiled habitats than at "nonoiled" sites 1 year after EVOS (Jewett et al. 1995), which is consistent with our observation that those fishes were more prevalent in the diets of otters from oiled areas in 1990 (Bowyer et al. 1994). The delay in dietary changes in otters living in the oiled area until summer 1990 could have resulted from oil moving from intertidal to subtidal habitats during that time (Bowyer et al. 1994). Nearshore (<30 m depths) demersal fishes exhibited continuing exposure to oil through the first 3 years after the spill (Collier et al. 1996, Laurand and Haldorson 1996). Overall reductions in bony fishes in the diet of otters on oiled sites (Bowyer et al. 1994) was likely most important to their ecology, and may have resulted in the lower body mass observed in otters inhabiting oiled areas (Fig. 3).

Increases in crustaceans in diets on oiled sites may have reflected either lower availability of fishes (the preferred diet of otters; Larsen 1984, Stenson et al. 1984, Bowyer et al. 1994), or alternatively a reduction in the diving and foraging abilities of otters as a result of direct exposure to hydrocarbons (Fig. 1; Ben-David et al. 2000). Indeed, Kruuk (1995) observed that European otters that were less efficient in their foraging ability fed more on crabs, whereas otters with better foraging ability or potentially in better health, existed on a diet of marine fishes.

Although comparing results from stable isotope analysis with those of prey remains in feces cannot be done directly (Ben-David and Schell 2001), our observation that stable isotope ratios of river otters captured in Herring and Jackpot bays in 1996–97 were similar indicated that no dietary differences occurred between those 2 areas. Several species of fishes in this system have similar

isotopic signatures (Ben-David et al. 1998b), thus otters feeding on different amounts or species of fishes could have similar isotopic values (Ben-David 1997a, 1997b; Blundell et al. 2002). Nonetheless, crabs have a different isotopic signature than any of the fishes and an increased consumption of crabs would have resulted in different isotopic signatures in otter tissues (Ben-David et al. 1998b).

Our analyses of SCUBA transects in 1996–97 revealed similar distributions and density of fish species in both study areas but differences in fish densities between years (Table 8, Fig. 10). This observation fits well with the annual changes we observed in stable isotope values of otter hair (Fig. 8), lending further support to the conclusion that lack of differences in isotopic values between areas indicates similar diets for otters in oiled and "nonoiled" areas in 1996–97. Thus, we conclude that in contrast to our earlier analyses, we observed no evidence of differences in diets of otters inhabiting oiled and "nonoiled" areas in 1996–97, providing further evidence of recovery. Indeed, evidence exists that intertidal communities are recovering from the effects of EVOS (Skalski et al. 2001, Page et al. 2002).

Use of Landscape

We demonstrated differences in habitat selection by otters inhabiting oiled and "nonoiled" areas in the early part of our study (Fig. 11; Bowyer et al. 1995). The variables that were diagnostic in identifying latrine sites, and thus habitat selection by otters, indicated otters avoided oiled beaches; otters on oiled areas selected steep tidal slopes and large rocks where oil did not accumulate (Bowyer et al. 1995; Fig. 11). Although differences in habitat selection between oiled and "nonoiled" sites still occurred in 1996–97, none of those variables could be associated with avoidance of oiled beaches. In addition, direction of selection (i.e., avoidance of vs. selection for) was identical for oiled and "nonoiled" sites, only the magnitude differed between areas (Fig. 11). No difference occurred between oiled and "nonoiled" areas in the mean value of tidal slopes at latrines. Furthermore, this value was identical to the mean tidal slope selected for by river otters in Esther Passage in 1990

(Table 9). That those differences between oiled and "nonoiled" areas diminished in our recent studies, is another measure of recovery (Fig. 11).

Larger home ranges on oiled compared with "nonoiled" areas in the early years of our research (Fig. 12) supported our observation that some shoreline habitats (Table 9) were avoided on oiled areas (Bowyer et al. 1995). That home-range sizes in Herring Bay declined between 1990 and 1997–99 (Fig. 13) indicated that otters during the later years no longer needed to avoid oiled shores. That outcome agrees with our observation that selection of habitat characteristics related to avoidance of oiled beaches (tidal slopes and rock size) no longer differed (Fig. 11). Therefore, previous avoidance of oiled shores likely resulted in increased home-range size for river otters, which in turn contributed to the dietary differences we observed in 1990 (Bowyer et al. 1994). Otters traveling over large areas likely were forced to forage on more sedentary prey to compensate for reduced foraging efficiency (Fig. 1; Bowyer et al. 1994, Ben-David et al. 2000), as manifested by the differences in diet between oiled and "nonoiled" areas in the early phase of our study.

Demography

Although our early studies indicated a 3-fold difference in the abandonment of latrines on oiled compared with "nonoiled" areas (Duffy et al. 1994a), our more recent research showed that other factors, in addition to population density, were involved in that process. We caution that abandonment may provide a biased index to population size. Other studies of otters used feces deposition at latrine sites as an index of population size (Crawford et al. 1979, Strachan et al. 1990, Serfass et al. 1993), although the use of fecal deposition at latrines has been controversial (Mason and Macdonald 1987, Kruuk and Conroy 1987). Clearly, more research on the role of social behavior and its effects on the deposition of feces by otters and other mustelids is needed. Scent-marking behavior among mustelids may vary across and within species in relation to social systems, habitat, and population density (Hutchings and White 2000).

In our early studies, no differences in population estimates were detected between oiled and "nonoiled" areas (Testa et al. 1994). We cautioned, however, that estimates for river otters prior to the oil spill were unavailable. Furthermore, no measurable decline in otter numbers on the oiled site (Herring Bay) was detected through 1 season but that observation did not rule out the possibility that substantial mortality might have occurred in that area prior to obtaining that estimate. Alternatively, our estimates could have been conducted too early and substantial mortality could have occurred after we conducted our sampling in 1990.

Mortality of river otters after 1990 could have been the result of interactions between direct physiological damage from chronic exposure to oil, decreases in diving and foraging efficiencies (Tarasoff et al. 1972, Fish 1994; Ben-David et al. 2000), and increases in energy demands from the need to avoid oiled beaches (i.e., larger home ranges; Kruuk 1995, Powell et al. 1997). These combined processes may have resulted in the observed reduction in body mass of otters from oiled areas (Fig. 3), associated increases in levels of fecal porphyrin (Smith and El-Far, 1980; Taylor et al. 2000a), and an increase in the probability of mortality. Supportive data on reductions in body condition of sea otters following EVOS are available (Rotterman and Monnett 2002).

Calculated densities of river otters in Herring Bay in 1997 based on population enumeration result in an estimate of 1 animal per 2.2 km of shoreline. In contrast, density estimates obtained from the population reconstruction are 1 animal/1.5 km of shoreline. Both estimates are higher than those reported for river otters in freshwater systems (1 otter/2.7–5.8 km of waterway; Melquist and Hornocker 1983, Reid et al. 1987). We believe it unlikely that such densities of otters could be maintained under continuous exposure to hydrocarbons even in marine systems, where availability of forage is higher than that of freshwater habitats (Kruuk 1995).

Our enumeration of populations for oiled and "nonoiled" areas in 1997 indicated that densities of otters were lower in Jackpot Bay ("nonoiled") than in Herring Bay (oiled). Furthermore, the minimum number of river

otters alive in Herring Bay in 1997 was within the upper values of the confidence interval of earlier (1990) estimates. Another analysis (population reconstruction from age structure) yielded even higher values for otters in that area than previously estimated. Comparing the estimates from 1990 with the minimum number alive and the population reconstruction in Herring Bay in 1997 indicated a growth of 1.3–6.4 % per year. Moreover, most of those otters (animals <6 years old; 12 of 13) were recruited following EVOS (Fig. 14). Numerous studies on mustelids demonstrate reductions in fecundity and high mortality of neonates in animals exposed to hydrocarbons or similar compounds such as Polychlorinated Biphenyl (PCB; Bleavins et al. 1980). A reduction in fecundity as a result of hydrocarbon exposure of the mother also was pronounced in a second generation of captive mink (Mazet et al. 2001). Effects of hydrocarbons on reproduction in river otters are not well studied, and outcomes for otters may differ from other mustelids (Wren 1991). Nonetheless, recruitment of river otters for most cohorts on oiled areas following the spill (Fig. 14) is opposite of that expected from lingering effects of oil, and likely indicates recovery.

We derived theoretical values of $\lambda = 1.24$, and $r = 0.212$ for river otters. This estimate likely approaches the reproductive potential (r_{\max}) for the species. We hypothesize that the rate of recovery for river otters in Herring Bay is less than maximal, potentially because we estimated number of otters in 1990 before a decline occurred. Moreover, recovery could have occurred before we began sampling in 1997. Indeed, the r_{\max} we calculated for river otters would have allowed 20 otters in 1991 (i.e., one-half the number of otters estimated in 1990) to reach a population size of 58 animals by 1996. Our data on age structure and survivorship indicate that recruitment and survival were not depressed in the later phase of our study. Ultimately, we would expect otters to approach some pre-spill equilibrium with their environment (data that are not available), which would explain our relatively low calculated rates of annual increase (1.3–6.4%).

Our analysis of population growth based on recruitment assumed no immigration or

emigration occurred in Herring Bay between 1990 and 1997. That assumption, however, may be invalid. In a companion study, Blundell et al. (2002b) investigated relatedness (Queller and Goodnight 1989) and gene flow (Cornuet et al. 1999) using DNA microsatellite analysis on blood samples collected from river otters captured in 1996–98. That analysis indicated that relatedness among river otters in Prince William Sound was generally low (average relatedness coefficient R ranged between 0.05 and 0.14), but animals in Jackpot Bay were more closely related to each other (average $R = 0.14$) than animals captured in Herring Bay (average $R = 0.06$; Blundell et al. 2002b). This lower relatedness among animals in our oiled site may have resulted from colonization of Herring Bay by migrants from other locations in Prince William Sound.

The lack of difference in our indirect measures of recruitment (i.e., age structure; Fig. 14) is supported by our estimates of survivorship, which did not differ between areas (Fig. 15). Our sample sizes for survivorship analysis were smaller than recommended (Pollock et al. 1989), likely reducing our ability to detect differences between areas. That survivorship was uniformly higher on the oiled area, however, indicated that effects of oiling were not manifested by high mortality in that population. In addition, estimates of survival for both areas were similar to those reported for river otters in Oregon (about 75%; Tabor and Wright 1977), and wild European otters in Shetland (about 85%; Kruuk and Conroy, 1991). Survivorship of our otters was also similar to that of wild-caught river otters reintroduced in North America (46–91%; Erickson and McCullough 1987, Greiss 1987, McDonald 1989), and wild caught and re-introduced European otters in Sweden (79%; Sjoasen 1996). Thus, all our demographic parameters indicate that the initial damage to river otters from the oil spill had diminished by the end of our study, and otters likely have recovered, regardless of whether recruitment of individuals into the oiled area was a result of reproduction or emigration.

Potential Routes for Intermittent Exposure

Because the physical properties of ingested

oil affect assimilation of hydrocarbons by animals (Ormseth and Ben-David 2000), understanding the route of exposure to oil hydrocarbons is important. Ormseth and Ben-David (2000) reported that ingestion of crude oil as nondispersed molecules (e.g., from an animal grooming its coat after swimming through an oil slick) resulted in increased passage rate of digesta and reduced assimilation of hydrocarbons. In contrast, ingestion of oil in the form that might occur in prey tissues may result in greater assimilation of hydrocarbons by the predator (Ormseth and Ben-David 2000). Thus, clarifying the potential routes of exposure is imperative to understanding how response to that exposure may manifest itself in the studied populations.

The most likely source of remaining oil in Prince William Sound was the 8–16% of 39,000 metric tons buried in marine sediments by a storm on the 3rd day following the spill (Wolfe et al. 1994). Oil is degraded by aerobic microorganisms (Braddock et al. 1995, 1996), which would have little opportunity to detoxify crude oil until it was uncovered and released by tides, currents, and winds in the Sound. Oil buried only 15 cm below ground persisted for 20 years without degrading substantially in terrestrial systems (Collins et al. 1993). Moreover, ultra violet light may enhance the toxicity of weathered oil, including some polycyclic aromatic compounds, beyond that observed under laboratory conditions; toxicity may be increased markedly in intertidal zones (Barron and Ka’Aihue 2001) where river otters concentrate their activities (Bowyer et al. 1995). Thus, while grooming, river otters may ingest previously buried and resuspended oil that accumulated on their fur. European otters spent substantial time grooming (Kruuk 1995), and our observations suggest the same for river otters. Oil recovered from the pelage of river otters in 1997 (Duffy et al. 1999b) supports this as a potential route of exposure.

Another potential route of exposure in otters may be through the consumption of prey. The presence of crude oil in mussel (*Mytilus* spp.) beds throughout western Prince William Sound was noted from 1990 to 1998 (Short et al., 1996, Carls et al., 2001; J. Short, NOAA, Juneau, Alaska, personal

communication). Indeed, mussels occurring in oiled areas continue to exhibit metabolic signs of stress 10 years following the spill (Downs et al. 2002). This source, however, is not likely to be the primary route for exposure for river otters because invertebrates compose only a small portion of otter diets (Larsen 1984, Stenson et al. 1984, Bowyer et al. 1994). Moreover, otters inhabiting areas with oiled mussel beds did not respond with elevated levels of Hp or IL-6 *ir* in 1992 (Duffy et al. 1994b). Alternatively, otters may be exposed to oil through consumption of fishes. The extent of that exposure, however, will depend on the ability of fishes to metabolize hydrocarbons (Woodin et al. 1997), and the time elapsed between the exposure of fishes and the ingestion of those fishes by otters. Recent investigation documented the occurrence of P450-1A in masked greenling (*Hexagrammos octogrammus*) collected in Herring Bay (Jewett et al. 2002). Whether hydrocarbons that occur in fishes are passed up the food chain and whether such exposure would be of sufficient magnitude to elicit P450-1A response in otters are uncertain and merit further investigation.

Synthesis

Taylor et al. (2000a) performed meta-analysis to examine the response of a suite of physiological variables from river otters collected in the early phase of the study, and concluded that the weight of evidence indicated river otters were injured by the spill. We likewise used that method to combine probabilities from a wide array of response variables collected in both phases of our study. Those analyses indicated that the initial injury no longer could be detected in the later phase (Table 10), indicating recovery of river otters from effects of EVOS. This is particularly evident when considering that our reference sites were lightly oiled rather than “nonoiled” (Stringer et al. 1992). Although diagnostic biomarkers, including Hp and IL-6 *ir*, fecal porphyrins, and body mass, all were consistently higher on oiled compared with “nonoiled” areas in our early studies (Figs. 4, 7, and 3, respectively), data for otters inhabiting presumably “nonoiled” sites also exhibited a pattern consistent with initial exposure to, and recovery from the effects of EVOS. Consequently, our data are

best interpreted as differences in response of river otters to severity of exposure to petroleum hydrocarbons. Accordingly, our comparisons provide a conservative analysis of damage and recovery of river otters.

Injury to river otters from EVOS could have been caused directly from toxicity of petroleum hydrocarbons or indirectly from damage to the nearshore ecosystem (Fig. 1). Nonetheless, both pathways may be interacting. Ben-David et al. (2000, 2001*b, c*) determined that chronic exposure to low doses of weathered crude oil, under controlled conditions, resulted in physiological damage, especially reduction in hemoglobin levels (and associated hematocrit and red blood-cells), reduction in white blood-cells, and elevation in several liver enzymes, Cytochrome *P450-1A1*, and *IL-6* *ir*. Further, this physiological damage (especially the reduction in hemoglobin) led to an increase in energetic costs of terrestrial locomotion (up to 40%), a decrease in aerobic dive limit (from 51 to 45 seconds), and a potential increase in foraging time (up to 64%), because of a decrease in total length of submergence during each foraging bout (Ben-David et al. 2000). Thus, physiological damage from exposure to crude oil could result in a decrease in body condition in free-ranging river otters. Indeed, we documented a reduction in body mass (controlled for age and sex classes) for otters live-captured in oiled areas of the Sound in the early phase of the study.

Furthermore, constraints imposed by oiling on diving behavior of otters likely will alter their diets. We would expect otters to concentrate on prey that potentially have a high rate of capture (i.e., prey that are slow moving, easily detected, or abundant). Again, we documented that change in diets of otters from oiled shores resulted mostly from a reduction in prey species and an increase in consumption of slow moving prey such as crustaceans (Bowyer et al. 1994). Nonetheless, changes in prey availability or avoidance of oiled beaches (i.e., selection of tidal slope) with an associated increase in home-range size could have caused similar changes in those behavioral responses of otters (Fig. 1).

Ben-David et al. (2002) demonstrated that levels of hemoglobin, which were indicative of incomplete rehabilitation in oiled captive

river otters, were related to post-release survival of those individuals. Indeed, in that study, animals with lower levels of hemoglobin perished soon after release and more experimental animals died of starvation than wild otters during a period of potential food shortage (Ben-David et al. 2002). Thus, physiological damage from oiling can negatively affect survival of oiled free-ranging river otters, regardless of prey availability. That we detected no differences in age structure and survival in otters from oiled and "nonoiled" areas of our study indicates that river otters in Prince William Sound have recovered from effects of EVOS.

Initial injury and subsequent recovery of river otters from EVOS likely resulted in cascading effects in the terrestrial system in Prince William Sound. Number of animals on the landscape would have determined the amount of nutrients transported from sea to land. For example, Ben-David (unpublished data) calculated that a density of 1 otter/2.7 km of shoreline (Reid et al. 1987) would result in an average deposition of 754 kg/ha/year of marine-derived nitrogen at latrines sites. In contrast, a density of 1 otter/1.3 km of shoreline (Testa et al. 1994) would result in an average deposition of 1,567 kg/ha/year nitrogen at latrines sites, a >100% increase in fertilization of terrestrial vegetation. Otter latrines are distributed along substantial stretches of coastline (Testa et al. 1994, Bowyer et al. 1995, Ben-David et al. 1998*b*), and hold the potential to influence far greater areas of the terrestrial environment near the coast than point sources of nutrient input surrounding streams (Ben-David et al. 1997*b*, 1998*a*). Changes in fertilization from feces of river otters may have a substantial effect on community composition of the beach-fringe forest (Ben-David et al. 1998*b*). Nonetheless, even smaller changes in otter densities, such as those we observed, may substantially alter the terrestrial ecosystem. Further research on interactions between pollution, populations, and landscape use by individuals and their effects on the land-margin system are warranted.

MANAGEMENT IMPLICATIONS

Use of biomarkers, including blood panels with numerous variables, to assess the

well being of free-ranging fish and wildlife populations has become widespread (Peakall 1992, Stegeman et al. 1992, Akins et al. 1993). Undeniably, biomarkers have several important advantages as a method for assessing the status of wildlife populations. First, most of these measures can be obtained with nondestructive sampling. Second, biomarkers may yield subtle information concerning the status of the population that cannot be obtained from gross necropsy or, in some instances, even sophisticated laboratory procedures (Zentano-Sabin et al. 1997). Third, some methods, such as analysis of fecal porphyrins, do not require capture or handling of individuals. Finally, biomarkers can be quantified and do not require subjective assessments based on experience to determine the health of individuals.

We documented that interpretations based on the physiological state of individuals may not be appropriate for making inferences about populations. Epidemiologists long ago embraced the science of population ecology in understanding the spread of diseases (Anderson and May 1985, Bacon 1985), and we agree with Caswell (1996) that the time is at hand for those who examine blood values and other biomarkers of individuals from wild populations to make a similar transition. We offer several standard methodologies with strong empirical underpinnings to aid in that process. We do not claim to have solved all of the existing difficulties with this complex problem—much remains to be accomplished. Nonetheless, we believe our approach offers an important first step in understanding how such data should be analyzed and interpreted.

We do not believe that a single biomarker will be sufficient to monitor the health of populations. Different causations can induce or elevate multiple biomarker systems (Ben-David et al. 2001b). Differences between and among species, sexes, age classes, reproductive status, physical condition, and other variables can complicate interpretation of biomarkers. For this reason alone, several systems for assessing status of populations are desirable, especially when biomarkers vary in their sensitivity to a particular stimulus or challenge. Likewise, that some biomarkers are more general (e.g., haptoglobin) and others more specific (e.g., P450-

1A) is a further reason to use them in concert. Difficulties in knowing which biomarkers to use to answer a specific question is the reason that so many different biomarkers are employed, and highlights the need for methods that allow for reductions in the dimensionality of those data, such as PCA.

We caution that successful interpretation of biomarkers may rely as much on an appropriate sampling design, including considerations of scale, as on physiological responses of animals. Without a sampling design to address a specific hypothesis, the likelihood of obtaining reliable knowledge (*sensu* Romesburg 1981) is nil. The particular objectives of the study will dictate the biomarkers required. Moreover, we advocate the use of sentinel and keystone species, such as river otters, to assess effects of environmental pollution. Seldom is it possible to determine the consequences of a calamity such as the *Exxon Valdez* oil spill on all links in an ecosystem. Use of sensitive and important components of the ecosystem allow for the initial assessment of pollution and provide a barometer for recovery.

Finally, integrating individual-based and population-level studies was essential to our understanding of processes and responses of a sentinel and keystone species to environmental pollution. We linked the use of biomarkers with the ecology and behavior of river otters (Fig. 1). To our knowledge, such an integration of disciplines to answer questions about effects of environmental pollution is rare. We often gained insights from 1 approach when others failed to provide clear-cut answers. Our study design allowed us to document chronic effects from EVOS on river otters when other studies were entrained exclusively on acute outcomes that could be related directly to mortality (Peterson 2001). We now know that such a narrow view of environmental pollution is short sighted, and hope that future studies of catastrophes such as EVOS, will incorporate a broader, more long-term ecosystem-based approach in their initial design.

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APPENDICES

Appendix A. Sample sizes of live-captured river otters

In 1989, we captured 7 otters (3 males, 4 females) in Herring Bay (oiled), and no otters in the "nonoiled" area. In 1990, 7 otters were captured in Herring Bay (all males) and 9 otters (7 males, 2 females) were captured in Esther Passage ("nonoiled"). In 1991, 12 otters (4 males, 8 females) were captured in oiled areas and 11 otters (2 males, 9 females) were captured in "nonoiled" areas. In 1992, we captured 10 individuals (9 males, 1 female) in oiled areas and in "nonoiled" areas 2 animals were captured (1 male, 1 female). In 1996, we captured 20 otters (12 males, 8 females) in Herring Bay, and 19 individuals (13 males, 6 females) were captured in the Jackpot Bay area ("nonoiled"). In 1997, 13 otters were captured in each of those areas with identical sex ratios (5 females and 8 males). In 1998, we captured 27 otters (22 males, 5 females) in oiled areas and 24 otters (18 males, 6 females) in "nonoiled" areas. During handling or short-

ly thereafter in 1989–90, 7 otters died but no histopathology reports were available. Two individuals captured in Jackpot Bay died during processing in 1997; post-mortem histopathology revealed that the juvenile male had pleuritis and the adult female had an abscessed ovary. These were the only mortalities of 111 individual otters captured 132 times from 1996 to 1998.

During 1989–91, a total of 27 otters were implanted with radiotransmitters, but due to premature failure of transmitters or mortality only 22 otters (15 males, 7 females) were available for radio-tracking (Testa et al., 1994; Bowyer et al., 1995). In 1996, we implanted 17 otters (12 males, 5 females) with transmitters in Jackpot Bay; no otters were telemetered in Herring Bay in that year. In 1997, 8 additional otters were equipped with radio-transmitters in Jackpot Bay (5 males, 3 females), and 12 otters were implanted with transmitters in Herring Bay (8 males, 4 females). In 1998, 9 otters received transmitters in Herring Bay (8 males, 1 female).

Appendix B. Abbreviations and units for blood-serum variables measured in river otters in Prince William Sound, Alaska, USA.

Variable name	Abbreviation	Units of measurement
Alanine Aminotransferase	ALT	U/L
Albumin	ALB	g/dL
Albumin/Globulin Ratio	AG Ratio	—
Alkaline Phosphatase	ALK PHOS	U/L
Aspartate Aminotransferase	AST	U/L
Blood Urea Nitrogen	BUN	mg/dL
Calcium	Ca	mg/dL
Chloride	Cl	mEq/dL
Cholesterol	CHOL	mg/dL
Cholesterol/High Density Lipid Ratio	CHOL/HDL	—
Creatine phosphokinase	CPK	IU/L
Direct Bilirubin	Dir Bili	mg/dL
Gamma Glutamyl Transpeptidase	GGT	U/L
Globulin	GLOB	g/dL
Glucose	GLU	mg/dL
Haptoglobin	Hp	mg hb-bound/100ml Hemoglobin [hb]
High Density Lipids	HDL	mg/dL
Interleukin-6 immunoreactive	IL-6ir	pg/ml
Lactate Dehydrogenase	LDH	U/L
Low Density Lipids	LDL	mg/dL
Phosphorous	P	mg/dL
Potassium	K	mEq/L
Serum Creatinine	SCREAT	mg/dL
Sodium	Na	mEq/L
Total Bilirubin	T. Bili	mg/dL
Total Protein	TP	g/dL
Triglycerides	TRIG	mg/dL
Uric Acid	UA	mg/dL
Very Low Density Lipids	VLDL	mg/dL

Appendix C. Abbreviation and units for whole blood variables measured in river otters in Prince William Sound, Alaska, USA.

Variable name	Abbreviation	Unit of measure
White Blood Cell Count	WBC	Th/cmm (thousand)
Red Blood Cell Count	RBC	m/cmm (million)
Hemoglobin	Hb	g/dL
Hematocrit = Packed Cell Volume	Hct or PCV	%
Mean Corpuscular Volume	MCV	fl
Mean Corpuscular Hemoglobin Concentration	MCHC	g/dl
Mean Corpuscular Hemoglobin	MCH	Pg
Red Cell Distribution Width	RDW	%
Platlet Count	PLAT	Th/cmm
Differential		
Segmented neutrophils	neuts	%
Lymphocytes	lymphs	%
Monocytes	mono	%
Eosinophils	eos	%
Basophils	baso	%

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