HORMONAL AND REPRODUCTIVE EFFECTS OF LOW LEVELS OF PETROLEUM FOULING IN MAGELLANIC PENGUINS (*SPHENISCUS MAGELLANICUS*)

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ABSTRACT.—Petroleum fouling has many deleterious consequences for marine vertebrates, ranging from increased energy expenditure to the death of the organism. We measured circulating levels of reproductive and adrenocortical hormones in Magellanic Penguins (*Spheniscus magellanicus*) that were partially covered with petroleum following a marine oil spill off the Patagonian coast, and in a non-oiled control group. Levels of luteinizing hormone, androgens and estradiol, but not progesterone, were lower in oiled penguins than non-oiled control birds. Corticosterone was higher in oiled than control females, but did not differ and was basal in males. Few of the pairs with an oiled partner later established nests with eggs. Even low levels of oil fouling in Magellanic Penguins appear sufficient to interfere with reproduction. Oiled penguins that were held captive for washing had elevated levels of corticosterone, and appeared to be stressed both by captivity and by the washing process. *Received 19 November 1993, accepted 27 May 1994.*

ENCOUNTERS WITH FLOATING PETROLEUM are harmful to marine birds and mammals in several ways. Direct physical effects include: (1) loss of thermal insulation (Erasmus et al. 1981, Bourne 1985) causing drastic increases in overall energy expenditure (Lambert et al. 1982, Culik et al. 1991); (2) loss of ability to float or fly (and thus ability to forage; Trivelpiece et al. 1984) resulting in increased energetic costs of locomotion (Culik et al. 1991); and (3) death from exposure. Penguins, because they live at the water surface, are particularly at risk of oil fouling (Culik et al. 1991, Gandini et al. 1994).

Petroleum ingested by the animal during attempts to clean itself can cause numerous physiological problems, including gastrointestinal lesions, renal and hepatic pathologies, hemolytic anemia, and increases in parasites (Fry and Lowenstine 1985, Fry and Addiego 1987, Gandini et al. 1994). In addition, suppression of the endocrine system by ingested petroleum has been experimentally demonstrated, including decreases in pituitary hormones (Harvey et al. 1982, Cavanaugh et al. 1983), gonadal steroids (Cavanaugh and Holmes 1982, Harvey et al. 1982), and adrenocortical steroids (Gorsline and

Holmes 1982, Gorsline 1982). Experimentally induced ingestion of petroleum also has been shown to reduce reproductive success in some breeding seabirds in the wild (Trivelpiece et al. 1984, Fry et al. 1986). Both physical and physiological effects can occur at low levels of oil fouling (Fry et al. 1986, Culik et al. 1991).

There have been no previous studies of the hormonal effects of oil fouling in accidentally oiled breeding birds at low levels of body coverage. We demonstrate suppression of luteinizing hormone and sex steroid hormones, and elevation of corticosterone in lightly oiled Magellanic Penguins (*Spheniscus magellanicus*) at the beginning of the breeding season following an accidental crude-oil spill.

METHODS

During the first week of September 1991, a crude-oil spill occurred in the waters north and east of the Magellanic Penguin colony at Punta Tombo, Chubut, Argentina (44°02′S, 65°11′W). Oiled penguins began to arrive at Punta Tombo in the second week of September 1991. Censuses indicated that approximately 17,000 penguins were affected by the spill (unpubl. administrative report, Dirección de Fauna y Flora Silvestres, Argentina 1991) in the coastal region including Punta Tombo. Heavily oiled, moribund penguins remained on the beaches at Punta Tombo and did not enter the breeding areas of the colony.

We studied lightly oiled animals that were not moribund and were encountered in the breeding areas,

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apparently attempting to reproduce. On 23 and 24 September, 1991 (ca. three weeks after the oil spill), blood samples were collected from 11 oiled and 11 non-oiled birds of each sex in matched circumstances (e.g. oiled female in nest with male matched with non-oiled female in nest with male; oiled male alone in nest matched with non-oiled male alone in nest). Sexes were determined by measurement of bill depth and bill length (Scolaro et al. 1983). The overall sample size ($n = 44$) was chosen to allow determination of circulating steroid-hormone concentrations in a single radioimmunoassay.

Locations of oiled penguins were marked in order to determine whether pairs with an oiled partner established nests and laid eggs. After we found that only 2 of the original 22 oiled birds had nests with eggs, the colony was searched for additional nesting oiled birds in early October 1991. Eight such additional nests were found: therefore, we were able to follow 10 nests (8 with an oiled male, 2 with an oiled female) until mid-December of 1991 to record the presence or absence of live chicks.

A temporary penguin-washing station was established at Punta Tombo following the spill. On 13 October 1991 (five weeks postspill and three to four weeks after individuals were captured), blood samples were collected from 10 captive birds. Six (3 males, 3 females) had been washed with oil dispersant, and 4 (2 males, 2 females) had not yet been washed; all 10 had been heavily oiled. Circulating levels of steroid hormones in healthy Magellanic Penguins decrease markedly over the first five to six weeks of the breeding season (Fowler 1993); therefore, blood samples from captive oiled penguins were compared with a second group of samples from free-living non-oiled penguins (8 males, 14 females) collected in the same week (8–16 October 1991). Nests of these non-oiled penguins also were used to compare reproductive success with nesting oiled penguins.

Blood samples were collected by jugular venipuncture using a pre-heparinized syringe. Penguins were then weighed and measured; in free-living oiled birds the percent of the body surface covered by oil was estimated to the nearest 5%. Blood samples were centrifuged, hematocrit was measured, and the plasma fraction was frozen at $-15°C$ at the site and later transported on dry ice to the laboratory for hormone assays. Duplication of label numbers on one sample required that two male samples (one oiled, one non-oiled) be discarded, resulting in a total sample size of 20 for free-living males.

Steroid-hormone levels were determined by the single-antibody radioimmunoassay of Wingfield and Farner (1975), as modified by Ball and Wingfield (1987). In a single assay, we separated and determined levels of the following five steroid hormones: progesterone (P), 5-α-dihydrotestosterone (DHT), testosterone (T), estradiol-17-β (E2), and corticosterone (B). Luteinizing-hormone (LH) levels were determined by the

TABLE 1. Product-moment correlations of percent coverage of body by crude oil with circulating hormone levels and body mass in Magellanic Penguins at Punta Tombo, Chubut, Argentina. Significant correlations in italics.

	Males		Females	
	r	P	r	P
Progesterone	0.606	0.117	0.030	0.930
DHT	−0.579	0.102	−0.559	0.074
Testosterone	−0.611	0.080	−0.446	0.169
Estradiol	0.350	0.430	−0.193	0.569
LH	−0.409	0.335	−0.231	0.494
Corticosterone	*0.785*	0.008	*0.803*	0.003
Body Mass	*−0.697*	0.025	−0.478	0.137

postprecipitation double-antibody radioimmunoassay of Follett et al. (1972), as updated by Sharp et al. (1987). After assays were completed, levels of testosterone and dihydrotestosterone in one oiled male and two non-oiled males were found to be an order of magnitude higher than found for any other of approximately 650 males. As these values were far outside the normal range, they were assumed to be a result of either contamination or laboratory error, and were discarded from further analysis.

Statistical analyses were conducted using SPSSPC+ (Norusis 1990). Pairwise comparisons of oiled versus non-oiled penguins were made using Mann-Whitney U-tests because variances were frequently unequal between groups. Reported probability levels are one-tailed for all tests involving hormone levels and body mass (suppression of these parameters was predicted), but two-tailed levels are reported for hematocrit values. Analyses of mass, sex steroids, and luteinizing hormone were conducted separately for each sex, as levels were expected to differ between males and females (Boswall and MacIver 1975, Wingfield and Farner 1993). We first tested for sex differences in hematocrit and corticosterone by ANOVA, and pooled sexes for further analysis where appropriate.

RESULTS

Free-living penguins.—The median percent body surface of free-living penguins covered with oil in our study was 20% ($\bar{x} = 30.5 \pm$ SE of 5.22%). Males and females did not differ significantly in oil coverage (35.8 vs. 23.2%, respectively; Mann-Whitney $U = 41.5$, $P = 0.35$). Sex steroids and luteinizing hormone were not significantly correlated with percent oil coverage in either sex (Table 1). However, plasma corticosterone concentration was strongly correlated with percent oil coverage in both sexes (males, $r = 0.785$, $P = 0.008$; females, $r = 0.803$,
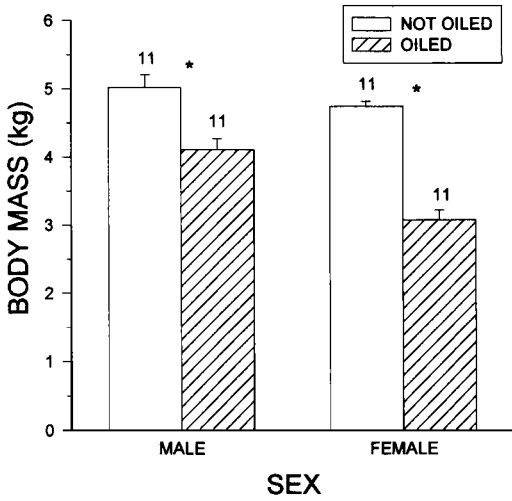
Fig. 1. Mean body mass in oiled and non-oiled male and female Magellanic Penguins. Whiskers indicate SE; sample sizes are shown above (*, $P < 0.05$).

$P = 0.003$). Body mass was inversely correlated with percent oil coverage in males ($r = -0.697$, $P = 0.025$), but was not correlated in females ($r = -0.478$, $P = 0.137$; Table 1).

Body mass of oiled penguins of both sexes was significantly lower than non-oiled penguins (males, 4.12 vs. 5.02 kg, $U = 65.5$, $P = 0.003$; females, 3.07 vs. 4.74 kg, $U = 66.0$, $P < 0.001$; Fig. 1). The mass of oiled males was 18.1% less on average than non-oiled males, whereas the mass of oiled females was 35.2% less on average than non-oiled females.

A two-way ANOVA showed no significant difference between the sexes in hematocrit levels ($P = 0.103$) and no interaction with oil effects ($P = 0.957$), so sexes were pooled for further analysis. Oiled birds had significantly higher hematocrit than non-oiled birds (44.0 ± 1.6% vs. 38.7 ± 1.5%; $U = 122.0$, $P = 0.013$).

Circulating levels of testosterone and dihydrotestosterone were significantly lower in oiled birds of both sexes (Mann-Whitney U-tests; $P < 0.025$ for T, DHT in males; $P < 0.004$ for T, DHT in females; Fig. 2). Estradiol levels in oiled females were significantly lower than non-oiled females ($U = 67.0$, $P < 0.001$; Fig. 3), but oiled and non-oiled males had similar and very low estradiol concentrations ($U = 48.0$, $P = 0.46$; Fig. 3). Luteinizing-hormone levels were lower in oiled compared to non-oiled females ($U = 6.0$, $P < 0.001$); a nonsignificant but suggestive difference was found for males, with oiled males
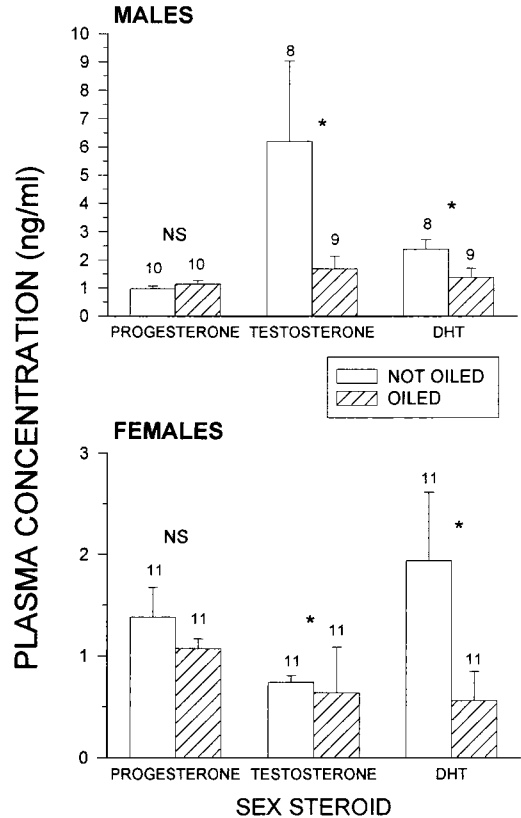

Fig. 2. Mean circulating levels of progesterone, testosterone, and 5-α-dihydrotestosterone (DHT) in oiled and non-oiled male and female Magellanic Penguins. Whiskers indicate SE; sample sizes are shown above. Mean value for DHT in oiled females is distorted upward by one female with an exceptionally high value (*, $P < 0.05$).

being lower ($U = 29.0$, $P = 0.056$; Fig. 4). Progesterone levels were similar in oiled and non-oiled penguins of both sexes (U-tests, $P > 0.20$ in both sexes; Fig. 2).

A two-way ANOVA of circulating levels of corticosterone showed a significant interaction between sex and oiling status ($P = 0.008$). Therefore, sexes were separated for further analysis. Corticosterone levels were significantly higher in oiled than non-oiled females ($U = 14.0$, $P = 0.002$; Fig. 5), but oiled and non-oiled males had similar levels ($U = 45.0$, $P = 0.70$; Fig. 5).

Only two of the original 22 oiled penguins had eggs in a nest in mid-October (both were males), compared to 16 of 20 nests of non-oiled pairs that were subjected to blood sampling prior to the egg-laying period ($X^2 = 21.5$, df = 1,
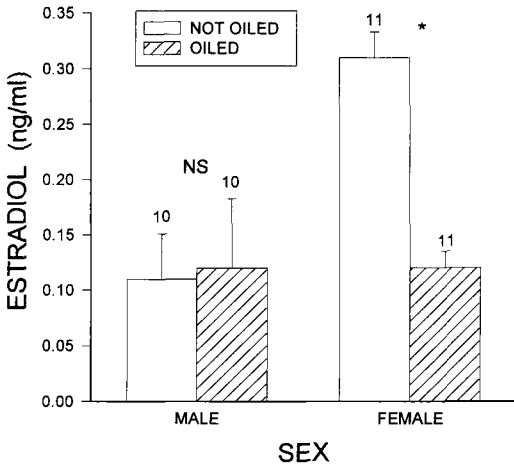
Fig. 3. Mean circulating levels of estradiol in oiled and non-oiled male and female Magellanic Penguins. Whiskers indicate SE; sample sizes are shown above (*, $P < 0.05$).
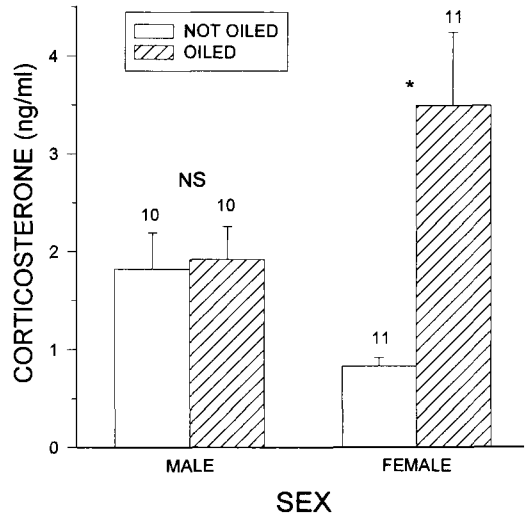
$P < 0.001$). However, in the additional set of 10 nests of oiled birds that were followed for reproductive success, 5 had live chicks in mid-December, compared to 7 of 13 comparable non-oiled nests in the same year ($X^2 = 0.03$, $P > 0.10$).
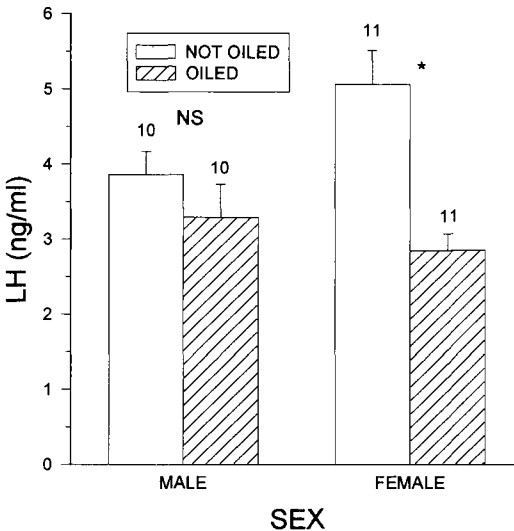

Fig. 4. Mean circulating levels of luteinizing hormone (LH) in oiled and non-oiled male and female Magellanic Penguins. LH levels are lower in oiled females; a suggestive but nonsignificant difference in same direction found for males. Whiskers indicate SE; sample sizes are shown above (*, $P < 0.05$).

Fig. 5. Mean circulating levels of corticosterone in free-living oiled and non-oiled male and female Magellanic Penguins. Whiskers indicate SE; sample sizes are shown above (*, $P < 0.05$).

Captive penguins.—Sex steroid and luteinizing-hormone levels in both washed and unwashed captive oiled penguins were low, but similar to levels in non-oiled free-living birds in the colony in general sampled during the same period (separate ANOVA's by sex, $P > 0.20$ in all cases). Male and female captive penguins had similar corticosterone levels, so values were pooled. Captive penguins had higher corticosterone levels than non-oiled penguins (ANOVA, $F = 77.1$, df = 2 and 29, $P < 0.001$) and washed penguins had higher corticosterone levels than unwashed (Scheffe's multiple range test, $P < 0.05$; Fig. 6).

Captive penguins of both sexes weighed less than non-oiled free-living birds sampled at the same time (separate U-tests, $P = 0.032$ for males, $P = 0.001$ for females; Fig. 7). However, the percent reduction in mass between captive and non-oiled females was greater than that between captive and non-oiled males (22.5 vs. 9.9%; $X^2 = 4.9$, df = 1, $P = 0.024$). Finally, captive birds of both sexes had hematocrit values similar to non-oiled birds of the same sex, although females had lower levels than males (two-way ANOVA; sex term, $P = 0.002$; oil term, $P = 0.335$).

DISCUSSION

Low levels of oil pollution are a chronic problem in coastal Patagonia, and oiled penguins
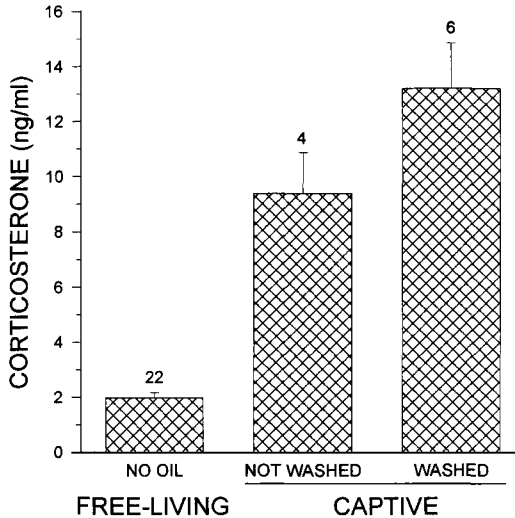
Fig. 6. Mean circulating levels of corticosterone in oiled penguins held captive for washing compared with free-living non-oiled birds sampled at same time. All three groups differ significantly. Captive birds were bled either before washing (NOT WASHED) or after washing (WASHED). Whiskers indicate SE; sample sizes are shown above.
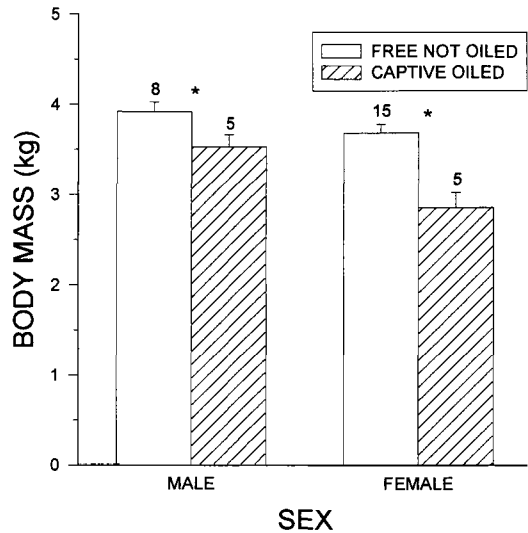

Fig. 7. Mean body mass in oiled male and female penguins held captive for washing, compared with free-living non-oiled birds sampled at same time. Whiskers indicate SE; sample sizes are shown above (*, $P < 0.05$).

appear on the beaches in virtually every year (Boersma 1987, Gandini et al. 1994). This spill occurred at precisely the time of year when all sex hormones were at their seasonal peaks prior to commencement of breeding (Fowler et al. 1994). Our study demonstrates that low levels of oil fouling suppress circulating levels of reproductive hormones and interfere with breeding, even though lightly oiled birds appear active and attempt to breed. Progesterone was the only sex hormone that was not suppressed in one or both sexes, and this may have been of nongonadal origin (Ball and Wingfield 1987).

Very few pairs that contained an oiled bird eventually laid eggs, although the few that did were as successful as non-oiled penguins in producing surviving chicks through mid-December. The low body mass of oiled penguins can be a problem because incubating birds fast for long periods during incubation (Boersma et al. 1990) and subsist on fat reserves. Body mass at the onset of incubation is an important determinant of eventual reproductive success (Fowler et al. 1994), as penguins with low fat reserves cannot fast as long and are more likely to abandon nests than heavier birds (Yorio and Boersma 1993).

Although both sexes of oiled penguins had significantly reduced body mass and levels of sex hormones, females appear to be more seriously affected than males. In particular, the proportional decreases in mass, LH level, and estradiol level were greater in oiled females than males, and the higher level of corticosterone in oiled females suggests that the energetic cost of oil fouling is higher in females. Ingestion of oil is known to inhibit egg formation (Grau et al. 1977), and the very low level of estradiol in oiled females is probably involved, as estradiol promotes vitellogenesis in the liver and yolk deposition in the ovary (Sturkie 1986).

The elevated levels of corticosterone in oiled females are curious in that most experimental studies have shown that ingested oil suppresses adrenocortical function (e.g. Gorsline 1982, Gorsline and Holmes 1982) by inhibition of synthesis and secretion of corticosterone, and also by increased metabolic clearance (Holmes 1984). However, Peakall et al. (1981) found elevated levels of corticosterone in oil-fed nestling seabirds. Oiled penguins face heavy energetic demands (Culik et al. 1991), and elevated levels are consistent with the role of corticosterone in mobilizing energy substrates (Hadley 1988). However, it is unclear if non-oiled penguins would respond to an equivalent

energetic challenge with similar or higher levels of corticosterone. The results of our study do not rule out some supression of adrenocortical function in oiled Magellanic Penguins.

Any suppression of adrenocortical function in oiled Magellanic Penguins cannot be complete, because heavily oiled captive penguins had much higher levels of corticosterone than non-oiled birds sampled during the same week. However, the response of non-oiled penguins to similar captive conditions is not known. Captive birds were housed out of doors at high densities (ca. 1 penguin/m² for washed birds and somewhat lower density for unwashed birds) and were fed by hand (initially by force feeding). However, human activity was not likely the primary cause of stress. Although routine handling (such as that for hand-feeding birds) can cause increases in corticosterone (Le Maho et al. 1992), these penguins had not been handled or fed on the day we collected blood samples, and handling times for captive penguins were similar to those for free-living birds. In addition, handling times in both groups typically were less than the 2-min lag period between initial capture and a detectable increase in plasma corticosterone in Magellanic Penguins (Fowler unpubl. data). On the day that blood samples were collected, the penguins had been captive for three to four weeks and were strongly habituated to people: most individuals readily approached people to beg for food. Captivity and the washing process appear to have been the primary stressors.

Chronically elevated levels of corticosteroids are associated with suppression of the activity of reproductive, immune and digestive systems (Munck et al. 1984, Sapolsky 1987, 1992). Thus, holding oiled penguins in captivity, especially at high density and for extended periods, may be harmful to their long-term health and survival; this effect is in addition to that of oil fouling per se.

Although the difference in hematocrit is not large (11.0%), the elevated level in free-living oiled birds of both sexes was surprising, as hemolytic anemia can be a consequence of oil-fouling in birds brought to washing centers, where it inhibits the recovery of washed birds (Fry and Addiego 1987). However, these penguins were sampled approximately two weeks after encountering the oil spill, and Fry and Addiego (1987) found anemia to be most pronounced prior to two weeks after oiling, with

recovery thereafter. The elevated levels in oiled birds may reflect a longer time spent on land (fasting), or less frequent visits to the ocean to drink, as oiled birds appear reluctant to enter the water (pers. obs.).

The long-term prognosis for future reproduction in lightly oiled seabirds is not well understood. There is some evidence of long-term suppression of breeding in oiled seabirds, whether washed or not (Morant et al. 1981, Fry et al. 1986). However, it is clear that low levels of oil pollution can seriously harm reproduction in seabirds and, in particular, can cause problems in species with low and/or variable reproductive rates (e.g. Fry et al. 1986, Boersma et al. 1990). Even at low levels the deleterious effects of petroleum on sex hormones and reproductive success are profound. Conservation efforts should stress prevention of oil pollution at all levels, from seepage to major spills.

LITERATURE CITED

BALL, G. F., AND J. C. WINGFIELD. 1987. Changes in plasma levels of sex steroids in relation to multiple-broodedness and nest site density in male starlings. Physiol. Zool. 60:191–199.

BOERSMA, P. D. 1987. Penguins oiled in Argentina. Science 236:135.

BOERSMA, P. D., D. L. STOKES, AND P. M. YORIO. 1990. Reproductive variability and historical change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. Pages 13–44 *in* Penguin biology (L. S. Davis and J. T. Darby, Eds.). Academic Press, San Diego, California.

BOSWALL, J., AND D. MACIVER. 1975. The Magellanic Penguin *Spheniscus magellanicus*. Pages 271–305 *in* The biology of penguins (B. Stonehouse, Ed.). Macmillan, London.

BOURNE, W. R. P. 1985. Oil and seabirds. Mar. Pollut. Bull. 16:85–86.

CAVANAUGH, K. P., A. R. GOLDSMITH, W. N. HOLMES, AND B. K. FOLLETT. 1983. Effects of ingested petroleum on the plasma prolactin levels during incubation and on the breeding success of paired Mallard ducks. Arch. Environm. Contam. Toxicol. 12:335–341.

CAVANAUGH, K. P., AND W. N. HOLMES. 1982. Effects of ingested petroleum on plasma levels of ovarian steroid hormones in photostimulated Mallard ducks. Arch. Environ. Contam. Toxicol. 11:503–508.

CULIK, B. M., R. P. WILSON, A. T. WOAKES, AND F. SANUDO. 1991. Oil pollution of Antarctic penguins: Effects on energy metabolism and physiology. Mar. Pollut. Bull. 22:388–391.

ERASMUS, T., R. M. RANDALL, AND B. M. RANDALL. 1981. Oil pollution, insulation and body temperatures in the Jackass Penguin (Spheniscus demersus). Comp. Biochem. Physiol. 69A:169–171.

FOLLETT, B. K., C. G. SCANES, AND F. J. CUNNINGHAM. 1972. A radioimmunoassay for avian luteinizing hormone. J. Endocrinol. 52:359–378.

FOWLER, G. S. 1993. Ecological and endocrinological aspects of long-term pair bonds in the Magellanic Penguin (Spheniscus magellanicus). Ph.D. dissertation, Univ. Washington, Seattle.

FOWLER, G. S., J. C. WINGFIELD, P. D. BOERSMA, AND R. A. SOSA. 1994. Reproductive endocrinology and weight change in relation to reproductive success in the Magellanic Penguin (Spheniscus magellanicus). Gen. Comp. Endocrinol. 94:305–315.

FRY, D. M., AND L. A. ADDIEGO. 1987. Hemolytic anemia complicates the cleaning of oiled seabirds. Wildl. J. 10:3–8.

FRY, D. M., AND L. J. LOWENSTINE. 1985. Pathology of Common Murres and Cassin's Auklets exposed to oil. Arch. Environ. Contam. Toxicol. 14:725–737.

FRY, D. M., J. SWENSON, L. A. ADDIEGO, C. R. GRAU, AND A. KANG. 1986. Reduced reproduction of Wedge-tailed Shearwaters exposed to weathered Santa Barbara crude oil. Arch. Environ. Contam. Toxicol. 15:453–463.

GANDINI, P., P. D. BOERSMA, E. FRERE, M. GANDINI, T. HOLIK, AND V. LIECHTSCHEIN. 1994. Magellanic Penguins (Spheniscus magellanicus) are affected by chronic oil pollution along the coast of Chubut, Argentina. Auk 111:20–27.

GORSLINE, J. 1982. The effects of South Louisiana crude oil on adrenocortical function. Pages 359–364 in Aspects of avian endocrinology: Practical and theoretical implications (C. G. Scanes, M. A. Ottinger, A. D. Kenney, J. Balthazart, J. Cronshaw, and I. C. Jones, Eds.). Grad. Studies Texas Tech Univ. 26. Texas Tech Univ., Lubbock.

GORSLINE, J., AND W. N. HOLMES. 1982. Suppression of adrenocortical activity in Mallard ducks exposed to petroleum-contaminated food. Arch. Environ. Contam. Toxicol. 11:497–502.

GRAU, C. R., T. E. ROUDYBUSH, J. C. DOBBS, AND J. WATHEN. 1977. Altered yolk structure and reduced hatchability of eggs from birds fed single doses of petroleum oils. Science 195:779–781.

HADLEY, M. 1988. Endocrinology, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

HARVEY, S., J. G. PHILLIPS, AND P. J. SHARP. 1982. Reproductive performance and endocrine responses to ingested North Sea oil. Pages 379–395 in Aspects of avian endocrinology: Practical and theoretical implications (C. G. Scanes, M. A. Ottinger, A. D. Kenney, J. Balthazart, J. Cronshaw, and I. C. Jones, Eds.). Grad. Studies Texas Tech Univ. 26. Texas Tech Univ., Lubbock.

HOLMES, W. N. 1984. Petroleum pollutants in the marine environment and their possible effects on seabirds. Pages 251–317 in Reviews in Environmental Toxicology I (E. Hodgson, Ed.). Elsevier, Amsterdam.

LAMBERT, G., D. B. PEAKALL, B. J. R. PHILOGENE, AND F. R. ENGELHART. 1982. Effect of oil and oil dispersant mixtures on the basal metabolic rate of ducks. Bull. Environ. Contam. Toxicol. 29:520–524.

LE MAHO, Y., H. KARMANN, D. BRIOT, Y. HANDRICH, J.-P. ROBIN, E. MIOSKOWSKI, Y. CHEREL, AND J. FARNI. 1992. Stress in birds due to routine handling and a technique to avoid it. Am. J. Physiol. 263 (Regulatory Integrative Comp. Physiol.):R775–R781.

MORANT, P. D., J. COOPER, AND R. M. RANDALL. 1981. The rehabilitation of oiled Jackass Penguins (Spheniscus demersus), 1970–1980. Pages 267–301 in Proceedings of the symposium on birds of the sea and shore (J. Cooper, Ed.). African Seabird Group, Cape Town, South Africa.

MUNCK, A., P. GUYRE, AND N. HOLBROOK. 1984. Physiological functions of glucocorticoids in stress and in their relation to pharmacological actions. Endocrinol. Rev. 5:25–44.

NORUSIS, M. J. 1990. SPSS/PC+ statistical data analysis. SPSS, Inc., Chicago.

PEAKALL, D. B., J. TREMBLAY, W. B. KINTER, AND D. S. MILLER. 1981. Endocrine dysfunction in seabirds caused by ingested oil. Environ. Res. 24:6–14.

SAPOLSKY, R. 1987. Stress, social status, and reproductive physiology in free-living baboons. Pages 292–322 in Psychobiology of reproductive behavior: An evolutionary perspective (D. Crews, Ed.). Prentice-Hall, New York.

SAPOLSKY, R. 1992. Neuroendocrinology of the stress response. Pages 287–324 in Behavioral endocrinology (J. B. Becker, S. M. Breedlove, and D. Crews, Eds.). MIT Press, Cambridge, Massachusetts.

SCOLARO, J. A., M. A. HALL, AND I. M. XIMENEZ. 1983.

The Magellanic Penguin (*Spheniscus magellanicus*): Sexing adults by discriminant analysis of morphometric characters. Auk 100:221–224.

SHARP, P. J., I. C. DUNN, AND R. T. TALBOT. 1987. Sex differences in the responses to chicken LHRH-I and II in the domestic fowl. Endocrinology 115: 323–331.

STURKIE, P. D. 1986. Avian physiology. Springer-Verlag, Berlin.

TRIVELPIECE, W., R. G. BUTLER, D. S. MILLER, AND D. B. PEAKALL. 1984. Reduced survival of chicks of oil-dosed adult Leach's Storm Petrels. Condor 86: 81–82.

WINGFIELD, J. C., AND D. S. FARNER. 1975. The determination of five steroids in avian plasma by radioimmunoassay and competitive protein-binding. Steroids 26:311–327.

WINGFIELD, J. C., AND D. S. FARNER. 1993. Endocrinology of reproduction in wild species. Pages 163–327 *in* Avian biology, vol. 9 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.

YORIO, P., AND P. D. BOERSMA. 1993. The effects of human disturbance on Magellanic Penguin behavior and breeding success. Bird Conserv. Int. 2:161–173.