

VARIATION IN FORAGING AND PARENTAL BEHAVIOR OF KING CORMORANTS

AKIKO KATO,^{1,6} YUTAKA WATANUKI,² ISAO NISHIUMI,^{3,7} MAKI KUROKI,⁴
PETER SHAUGHNESSY,⁵ AND YASUHIKO NAITO¹

¹National Institute of Polar Research, Itabashi, Tokyo 173-8515, Japan;

²Laboratory of Applied Zoology, Faculty of Agriculture, Hokkaido University, Sapporo, Hokkaido 060-8589, Japan;

³Department of Biology, Faculty of Science, Osaka City University, Sugimoto, Sumiyoshi, Osaka 558-8585, Japan;

⁴School of Polar Science, Graduate University for Advanced Studies, Itabashi, Tokyo 173-8515, Japan; and

⁵CSIRO Wildlife and Ecology, G.P.O. Box 284, Canberra 2601, Australia

ABSTRACT.—We studied sexual and individual differences in foraging and parental behavior of King Cormorants (*Phalacrocorax albiventer*) during the brood-rearing period at Macquarie Island. King Cormorants exhibit sexual dimorphism in size, with males being 16% heavier than females. Females foraged mainly in the morning and males in the afternoon. Five females were shallow divers (1.9 to 6.8 m), and seven females were deep divers (19.6 to 28.0 m); males dived deeper (15.6 to 44.2 m) than both groups of females. The amount of time spent on the bottom (“bottom time”) relative to the dive cycle was higher for shallow-diving females ($\bar{x} = 40 \pm \text{SD of } 13\%$) than for males ($\bar{x} = 26 \pm 4\%$) and deep-diving females ($\bar{x} = 27 \pm 3\%$). Total daily dive time and bottom time per day did not differ significantly among groups because shallow-diving females dived more often ($\bar{x} = 211 \pm 81$ dives per day) than males ($\bar{x} = 68 \pm 21$) and deep-diving females ($\bar{x} = 70 \pm 7$). Provisioning rate, trip duration, and proportion of time at sea did not differ significantly for males, deep-diving females, and shallow-diving females. Females, especially shallow divers, compensated for their shallow and short dives with more frequent dives. Consequently, male and female King Cormorants provisioned their chicks at similar rates despite large individual variation in foraging behavior. Received 4 January 1999, accepted 11 January 2000.

AMONG DIVING SEABIRDS, maximum depth and duration of dives appear to be related to body mass, probably because storage and use of oxygen are mass dependent (Cooper 1986, Kooyman 1989, Burger 1991). Cormorants are foot-propelled benthic feeders and have exceptional diving ability (Croxall et al. 1991; Wanless et al. 1993, 1995). Because they are sexually size dimorphic, cormorants might be expected to exhibit sexual differences in diving and foraging patterns. Sexual differences are known to occur in diving behavior (Kato et al. 1992, Wanless et al. 1995, Watanuki et al. 1996), daily activity patterns (Bernstein and Maxson 1984, Brothers 1985), duration of foraging bouts (Cooper 1985), and size of fish taken (Koffijberg and van Eerden 1995, Kato et al. 1996b) in several species of seabirds. However, the conse-

quences of body-size differences on foraging habits and parental behavior are unclear.

Male South Georgian Shags (*Phalacrocorax georgianus*) dive deeper and for longer durations than do females (Croxall et al. 1991, Kato et al. 1992), although this conclusion is based on a relatively small number of birds that carried time-depth recorders. Furthermore, South Georgian Shags show individual variation in diet and diving behavior (Wanless et al. 1992). Thus, it is necessary to have larger sample sizes of data on diving behavior, diet, nest attendance, and parental behavior to obtain a better understanding of the physiological and ecological consequences of sexual size dimorphism in cormorants. The King Cormorant (*P. albiventer*) is endemic to Macquarie Island and is closely related to the South Georgian Shag. We investigated diving and foraging behavior of a large sample of King Cormorants that were equipped with data loggers. We also observed nest attendance and parental activity to determine whether sexual and individual differences occurred in foraging and parental behavior.

⁶ E-mail: akato@nipr.ac.jp

⁷ Present address: Department of Zoology, National Science Museum, Hyakunin-cho, Shinjuku, Tokyo 169-0073, Japan.

STUDY AREA AND METHODS

Study area.—The study was conducted at the Handspike Point colony on subantarctic Macquarie Island (54°30'S, 158°57'E) from December 1993 to February 1994. The study site supported the largest breeding colony of the King Cormorants on the island, with 364 pairs nesting among boulders on the shoreline (N. Brothers unpubl. data). Brothers (1985) reported that most eggs were laid in the second half of October and that mean clutch size was 2.7 eggs. Most chicks hatched by late December and left the nest in late January; mean fledging success varied from 1.7 to 2.3 chicks per nest (Brothers 1985).

Diving behavior.—Diving behavior was measured with data loggers (19 mm diameter \times 70 mm long; weight = 30 g including battery; model KS-200DT, Little Leonardo Co. Ltd., Tokyo; see Watanuki et al. 1996) that were programmed to record depths at 5-s intervals and could store 250,000 registrations with 0.5 megabytes of flash memory. Birds were caught by hand at their nests. Data loggers were attached on the dorsal feathers with quick-set epoxy glue and cable ties. Data loggers were deployed on both members of 17 pairs during the nestling period: nine pairs on 1 January, six on 18 January, and two on 23 January. Loggers were recovered from 16 males and 14 females that we recaptured 6 to 13 days after deployment. One male abandoned his nest, three females lost their loggers before recapture, and seven loggers did not work properly. Therefore, we obtained data from 11 males and 12 females. Birds were weighed to the nearest 0.01 kg with a Pesola spring balance at deployment and recovery of loggers to calculate the rate of change in body mass. We determined the sex of birds by their vocalizations (Brothers 1985).

Analysis of diving data followed Watanuki et al. (1996). Cormorants descended rapidly (descent phase) to a certain depth, where they remained briefly (bottom time) and then ascended quickly (ascent phase) to the surface for respiration (surface time). We determined depth, duration, bottom time (duration at deeper than 80% of maximum depth), proportion of bottom time relative to the dive cycle (dive duration + surface time), descent rate, ascent rate, and surface time for each dive. Descent and ascent rates were calculated as depth changes per unit time during dives that had descent or ascent phases longer than 5 s. During foraging trips, cormorants made a series of dives in quick succession and stayed on or above the water for a long time between dive series. Thus, dives occurred in clusters, and a series of successive dives followed by a bout-ending criterion (BEC) was defined as a dive bout. To derive the BEC, we combined data from 23 birds and plotted a log survivorship curve of surface time between dives (see Watanuki et al. 1996: fig. 2). The inflection point of the curve is the BEC, indicating that for surface

periods longer than this point, the probability that the bird would dive was much lower than for shorter surface periods (Gentry and Kooyman 1986). Thus, a dive bout was a series of successive dives with intervals between dives of less than the BEC. We calculated bout duration, number of dives per bout, mean dive duration, mean surface time within bout, and surface time after bout for each diving bout. For each day, we also calculated number of dives, number of bouts, total bottom time, total dive time, and total bout duration.

Nest attendance.—To determine daily patterns of nest attendance, we conducted direct observations from dawn (0300 to 0400) until dusk (2100 to 2200) for 13 days (ca. every 4 days) in January and February at a distance of 5 m from the colony edge for 17 pairs with loggers and 10 pairs without loggers (control group). All 27 pairs were brooding chicks. Nest attendance was recorded every 15 min, and meal delivery rate, trip duration, and proportion of time at sea were calculated.

Chick growth and adult body mass.—Chick mass was measured every five days for the 10 control pairs from 31 December to 24 February and for 17 pairs with loggers during the period of logger deployment. Parents of the 10 control pairs were weighed between 26 and 31 December and again between 4 and 9 February to compare changes in body mass with those of birds equipped with loggers.

RESULTS

Effect of logger deployment.—Initial body mass of males was higher than that of females ($F = 146.6$, $df = 1$ and 50 , $P < 0.001$) and within sexes did not differ between logger-equipped and control birds ($F = 2.0$, $df = 1$ and 50 , $P = 0.27$; equipped males, $\bar{x} = 3.12 \pm$ SD of 0.23 kg; equipped males, $\bar{x} = 2.91 \pm 0.17$ kg; control females, $\bar{x} = 2.45 \pm 0.14$ kg; equipped females, $\bar{x} = 2.50 \pm 0.11$ kg). The rate of change in body mass did not differ significantly between equipped and control birds ($F = 2.6$, $df = 1$ and 45 , $P = 0.11$) nor between males and females ($F = 1.1$, $df = 1$ and 45 , $P = 0.31$; control males, $\bar{x} = -6.8 \pm 5.4$ g per day, $n = 10$; equipped males, $\bar{x} = -3.8 \pm 20.5$ g, $n = 16$; control females, $\bar{x} = -0.9 \pm 3.2$ g, $n = 10$; equipped females, $\bar{x} = -19.5 \pm 21.4$ g, $n = 13$). One of 26 chicks of logger-equipped pairs died during the deployment period, whereas 5 out of 16 chicks of control pairs died by predation, starvation, or unknown reasons between 31 December and 24 February.

Diving parameters.—We obtained data for 6,417 and 11,725 dives from 11 males and 12 fe-

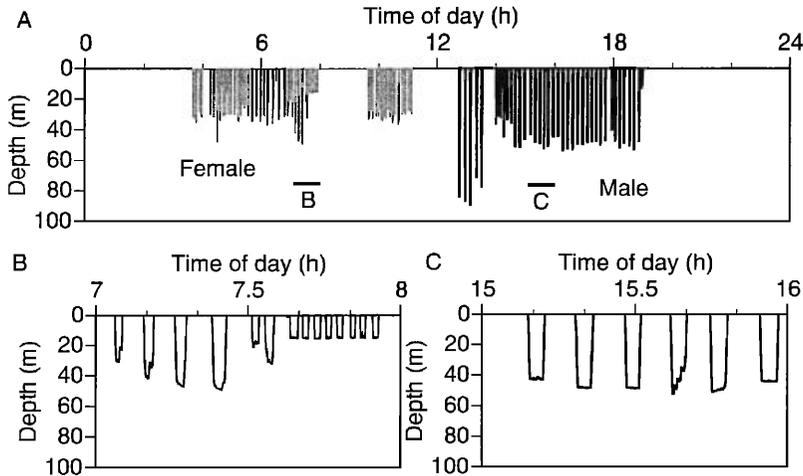


FIG. 1. (A) Diving record of a pair of King Cormorants on 3 January. Records indicated with horizontal bars were enlarged for the (B) female and the (C) male.

males, respectively. In a single dive, cormorants descended rapidly to a depth where they spent about 60 to 80% of the total dive duration and then ascended rapidly (Fig. 1A). Profiles of most dives had a ragged or flat bottom, and some dives had a vee-shaped bottom (Figs. 1B,C).

Mean and maximum dive depths of males were deeper than those of females (Table 1). Females fell into two groups based on dive depth: seven deep divers and five shallow divers (Fig. 2A). Neither body mass nor brood mass differed between these two groups (Table 1). Dives of males occurred over a wide depth range and peaked at 25 to 35 m, whereas those of deep-diving females peaked at 25 to 30 m and of shallow-diving females peaked at 0 to 10 m (Figs. 2B,C,D). Dive durations of shallow-diving females were shorter than those for males and deep-diving females, although those of the latter two groups did not differ from each other (Table 1). Bottom times of males and deep-diving females were longer than those of shallow-diving females, but the amount of bottom time relative to the dive cycle of shallow-diving females was significantly higher than that of the other groups (Table 1). Descent rates were slower than ascent rates (paired $t = -5.74$, $P < 0.001$; Table 1). Descent and ascent rates of males and deep-diving females were faster than those for shallow-diving females (Table 1).

Dive duration increased with dive depth, and the coefficients of determination (R^2) for

each individual was higher ($P < 0.05$) for males (range 0.61 to 0.85) and deep-diving females (0.72 to 0.86) than for shallow-diving females (0.13 to 0.77). Although bottom time and travel time (i.e. dive duration minus bottom time) increased with dive depth ($P < 0.05$), bottom time (range of R^2 0.09 to 0.71) varied more than travel time (range of R^2 0.12 to 0.93), especially for deeper dives. The proportion of bottom time relative to the dive cycle varied independently of dive depth, especially for shallow dives. Descent and ascent rates tended to increase for dives up to 20 m and seemed to converge at around 1.5 m per s as dives became deeper.

Dive bout.—Dives occurred in dive bouts (Fig. 1). BECs were calculated as 12 min for males, 8 min for deep-diving females, and 5 min for shallow-diving females. The durations of 48%, 64%, and 77% of dive bouts were shorter than 60 min, and the longest bout duration was 465 min, 293 min, and 259 min for males, deep-diving females, and shallow-diving females, respectively. Although mean bout duration was longer for males than for deep-diving and shallow-diving females, shallow-diving females made more dives per bout than the other two groups (Table 1). To determine variance components of dive depth, we performed a nested ANOVA with sex, individual, day, and bout as independent factors. The proportion of variance explained was 45.0% for sex, 25.1% for individual, 0% for day, and 16.1% for bout.

TABLE 1. Mass and diving data for King Cormorants.^a Values are $\bar{x} \pm SD$, with range in parentheses.

	Males (n = 11)	Deep-diving females (n = 7)	Shallow-diving females (n = 5)	F	P
	2.91 ± 0.17 (2.56 to 3.20) ^{A,B}	2.48 ± 0.10 (2.31 to 2.61) ^A	2.52 ± 0.12 (2.33 to 2.61) ^B	23.7	<0.001
	-0.8 ± 21.8 (-50.0 to 20.0)	-19.7 ± 21.6 (-66.7 to -4.6)	-23.8 ± 22.7 (-56.7 to -6.2)	2.6	0.10
	2.46 ± 0.93 (0.12 to 4.00)	2.82 ± 0.90 (1.71 to 4.08)	1.69 ± 1.50 (0.04 to 3.21)	1.7	0.21
	33.0 ± 8.9 (15.6 to 44.2) ^{A,B}	24.1 ± 3.4 (19.6 to 28.0) ^{A,C}	5.2 ± 2.0 (1.9 to 6.8) ^{B,C}	30.2	<0.001
	84.5 ± 16.5 (62.7 to 108.8) ^{A,B}	50.3 ± 11.0 (32.9 to 61.7) ^{A,C}	23.9 ± 8.8 (14.5 to 35.7) ^{B,C}	36.8	<0.001
	114.6 ± 29.3 (67.4 to 174.6) ^B	96.1 ± 19.5 (73.9 to 130.1) ^C	27.8 ± 10.9 (9.6 to 35.7) ^{B,C}	23.2	<0.001
	78.3 ± 21.6 (47.3 to 128.1) ^B	68.6 ± 19.5 (50.0 to 103.7) ^C	20.7 ± 10.1 (5.1 to 28.4) ^{B,C}	16.5	<0.001
	26.2 ± 3.6 (21.3 to 33.1) ^B	26.6 ± 2.7 (22.7 to 30.9) ^C	39.5 ± 12.9 (19.8 to 50.6) ^{B,C}	8.1	0.003
	1.30 ± 0.07 (1.16 to 1.39) ^B	1.27 ± 0.09 (1.11 to 1.40) ^C	0.45 ± 0.28 (0.06 to 0.79) ^{B,C}	69.3	<0.001
	1.56 ± 0.13 (1.21 to 1.71) ^B	1.51 ± 0.13 (1.27 to 1.67) ^C	0.49 ± 0.30 (0.26 to 0.93) ^{B,C}	65.6	<0.001
	96.8 ± 31.5 (58.1 to 147.8) ^{A,B}	64.4 ± 19.3 (35.1 to 94.7) ^A	35.8 ± 23.8 (9.9 to 62.5) ^B	9.5	0.001
	18.5 ± 5.2 (11.5 to 26.2) ^B	14.9 ± 3.8 (10.5 to 19.7) ^C	39.8 ± 20.6 (19.1 to 67.2) ^{B,C}	10.1	<0.001
	68.2 ± 20.5 (51.8 to 117.5) ^B	70.3 ± 7.2 (61.3 to 79.1) ^C	211.4 ± 81.2 (114.5 to 302.5) ^{B,C}	25.7	<0.001
	4.6 ± 1.0 (3.4 to 6.5)	4.3 ± 1.5 (3.1 to 6.6)	5.6 ± 0.8 (4.5 to 6.4)	2.3	0.13
	123.2 ± 15.5 (102.6 to 161.2)	111.4 ± 17.3 (88.3 to 136.2)	107.3 ± 68.2 (16.7 to 180.1)	0.5	0.63
	84.1 ± 13.7 (70.2 to 118.3)	79.4 ± 16.7 (60.2 to 108.8)	84.6 ± 54.4 (15.2 to 142.5)	0.1	0.93

^a Within rows, values with same letter in superscript are significantly different (post-hoc test; $P < 0.05$).

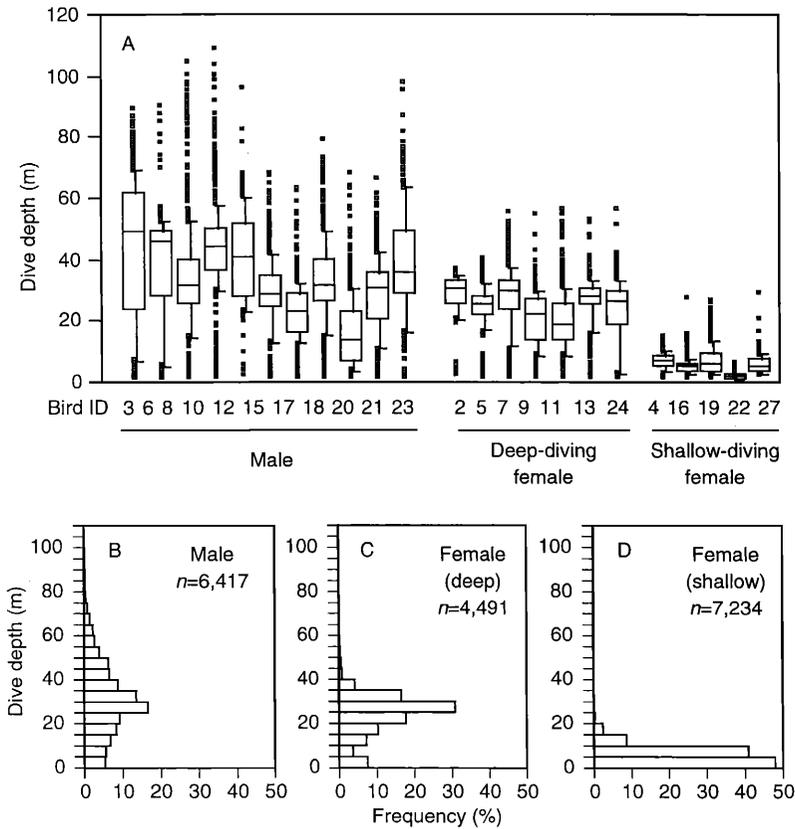


FIG. 2. (A) Distribution of dive depths for individual King Cormorants. The ends of boxes are quartiles and whiskers denote 10th and 90th quantiles. All data below the 10th and above the 90th quantiles are shown. The line across the middle of each box denotes the median. Frequency distributions of dive depth for (B) males, (C) deep-diving females, and (D) shallow-diving females. Data for individual birds are combined.

Although coefficients of determination were small, the subsequent surface time within dive bouts increased with dive duration ($R^2 = 0.15$ to 0.56 for males, 0.19 to 0.44 for deep-diving females, 0.01 to 0.18 for shallow-diving females; Figs. 3A,D,G). Coefficients of determination were larger when mean surface time within a bout was regressed on mean dive duration within a bout for males ($R^2 = 0.20$ to 0.69) and deep-diving females ($R^2 = 0.20$ to 0.76 ; paired $t = -4.05$, $P < 0.001$), except for shallow-diving females, for which the relationship was not significant (Figs. 3B,E,H). Interbout intervals were not correlated with the preceding dive-bout duration, except for three males and one deep-diving female (Figs. 3C, F, I). We found no tendency for dive duration to be shortened, nor for surface time to be prolonged, as the dive bout progressed.

Daily foraging pattern.—Males and females with and without loggers stayed at the colony during the night and were active from dawn until dusk. Males tended to stay at the colony in the morning and forage in the afternoon, and females did the reverse. This pattern of nest attendance occurred throughout the breeding season. Females dived principally from dawn to noon (89% of dives from 0300 to 1200; Figs. 4B,C), whereas males dived from noon to dusk (83% of dives from 1200 to 2100; Fig. 4A); males dived deeper than females at all times of day (Fig. 4).

Shallow-diving females made significantly more dives per day than did males and deep-diving females, whereas the number of bouts per day, total daily dive time, and total daily bottom time did not differ significantly among the three groups (Table 1).

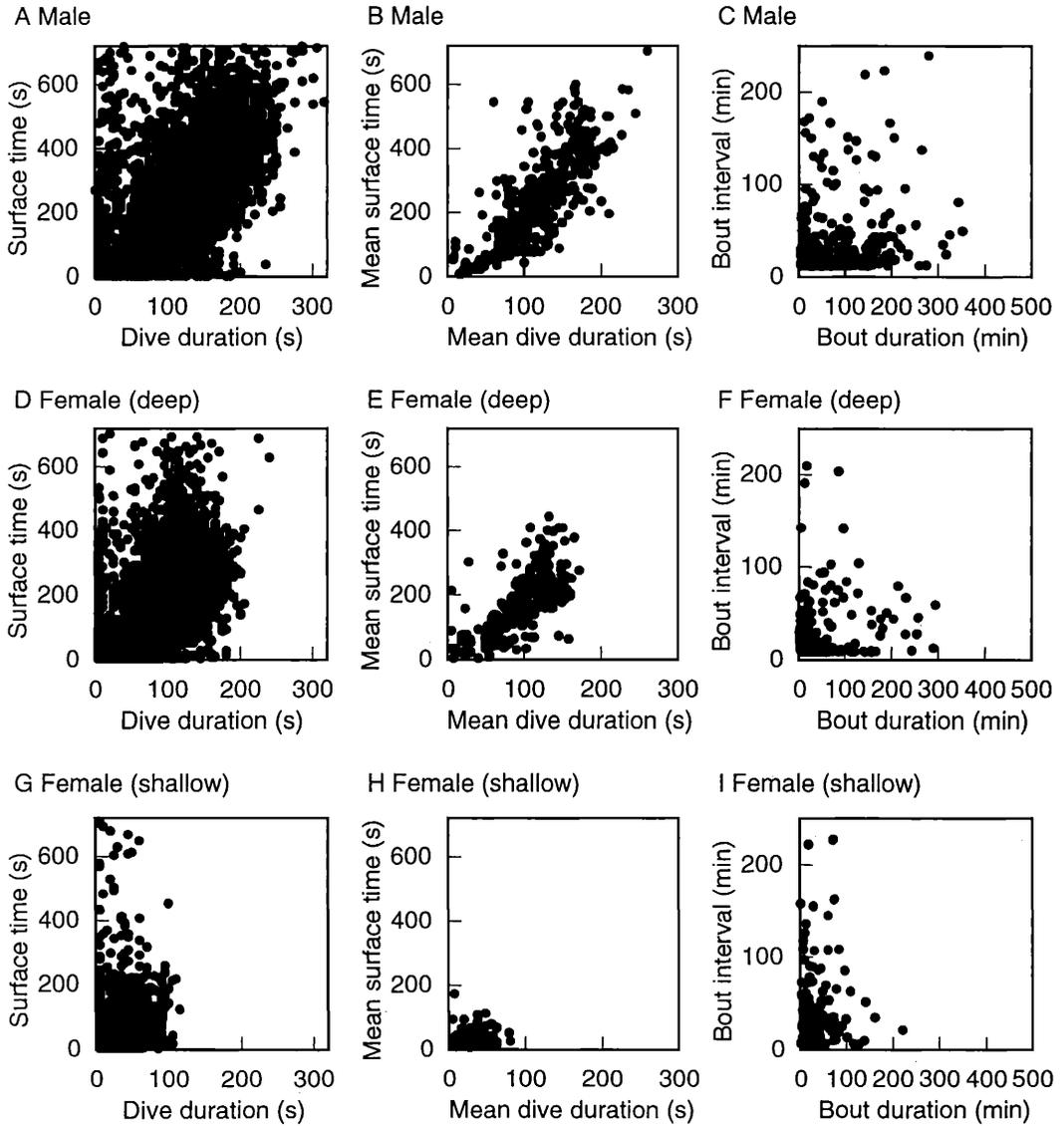


FIG. 3. Relationship between dive duration and surface time, mean dive duration and mean surface time within bout, and bout duration and subsequent interbout interval for male (A, B, C), deep-diving female (D, E, F), and shallow-diving female (G, H, I) King Cormorants. Data for individual birds are combined.

Foraging trips.—Meal delivery rate, trip duration, and proportion of time at sea did not differ significantly between control and logger-equipped birds or between males and females (Table 2). The proportion of time at sea was greater for deep-diving females ($\bar{x} = 47.0 \pm 7.1\%$, $n = 7$) than for shallow-diving females ($\bar{x} = 34.9 \pm 6.8\%$, $n = 5$; $F = 8.7$, $df = 1$ and 10 , $P = 0.014$), whereas trip duration and meal de-

livery rate did not differ for the two groups of females.

We examined parameters of foraging trips for which both observational and diving data were obtained. Mean trip duration for seven trips of shallow-diving females was significantly shorter than that for all individuals combined (Tables 2, 3). Deep-diving females made more bouts per trip than males, but the pro-

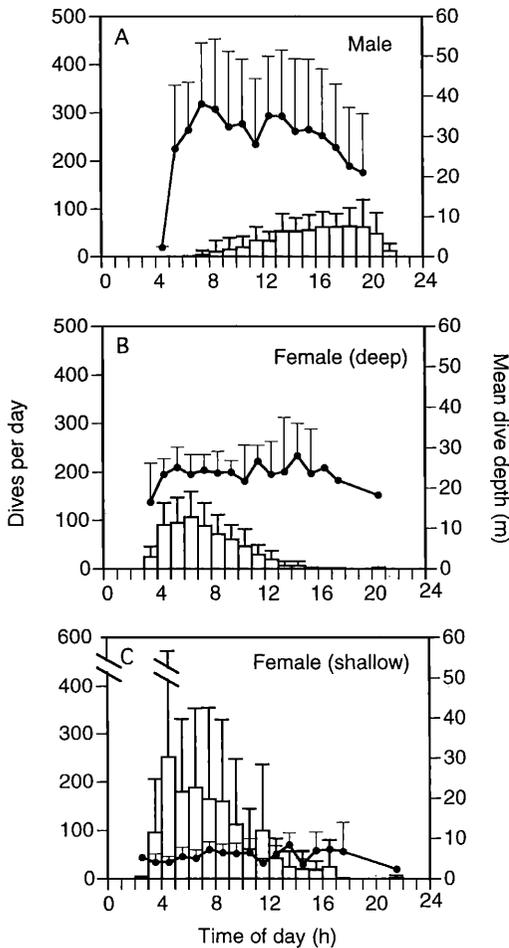


FIG. 4. Daily changes in the number of dives per hour (bars) and dive depths (lines) for (A) male, (B) deep-diving female, and (C) shallow-diving female King Cormorants. Whiskers denote 1 SD.

portion of total bout duration in trips did not differ for the two groups (Table 3). Total bout duration increased with trip duration ($r_s = 0.86$, $n = 58$, $P < 0.001$), but the number of

bouts and proportion of bout duration was not correlated with trip duration. Times from departure to first dive and from last dive to arrival at the nest did not differ among groups (Table 3). Time from departure to first dive was shorter than time from last dive to arrival for males (Mann-Whitney $U = 573$, $n_1 = 2$, $n_2 = 39$, $P = 0.008$), but these values did not differ significantly for deep-diving and shallow-diving females (Table 3). In most cases, bout intervals within trips were shorter than 30 min (Table 3).

To determine the effect of body mass on variation in diving behavior, we tested correlations of body mass on mean dive duration, maximum dive duration, mean dive depth, and maximum dive depth for 11 males and 12 females (Figs. 5A to D); correlations were not significant for either sex.

Correlations between brood mass and three characters (mean meal delivery rate, trip duration, and percentage of time at sea) were examined in five-day periods, because brood mass was measured over that time interval. We combined data from control and logger-equipped birds because no difference was observed between them. Meal delivery rate was significantly correlated with brood mass for females ($r_s = 0.29$, $n = 127$, $P = 0.001$) but not for males ($r_s = 0.09$, $n = 127$, $P = 0.33$). Although trip duration was not correlated with brood mass, the proportion of time at sea was correlated with brood mass for males ($r_s = 0.25$, $n = 127$, $P = 0.005$) and females ($r_s = 0.61$, $n = 127$, $P < 0.001$).

We examined correlations between mean number of dives per day, daily dive time, and daily bottom time in five-day periods with brood mass for males ($n = 22$), deep-diving females ($n = 16$), and shallow-diving females ($n = 9$). None of the correlations was significant ($r_s = -0.38$ to 0.68 ; all $P > 0.05$).

TABLE 2. Meal delivery rate, trip duration, and proportion of time at sea for male and female King Cormorants with ($n = 17$ of each sex) and without ($n = 10$ of each sex) data loggers. Values are $\bar{x} \pm$ SD. No significant difference existed between sexes or between control and logger-equipped birds (two-way ANOVA, $0.05 < P < 0.60$).

Variable	Logger-equipped		Control	
	Males	Females	Males	Females
Meal delivery rate (per day)	1.9 ± 0.6	2.1 ± 0.5	1.9 ± 0.6	2.3 ± 0.7
Trip duration (h)	4.7 ± 1.9	4.6 ± 1.5	4.4 ± 1.4	3.1 ± 1.3
Time at sea (%)	39.9 ± 5.4	44.7 ± 9.6	39.6 ± 6.0	37.3 ± 10.2

TABLE 3. Data on foraging trips and foraging bouts of King Cormorants.^a Values are $\bar{x} \pm SD$, with *n* in parentheses.

Group	Trip duration (h)	No. of bouts	Total bout duration (min)	Bout duration (%)	Time to first dive (min)	Time from last dive (min)	Bout interval (min)
Males	4.5 ± 1.79 (39) ^A	1.8 ± 0.92 (42) ^A	189.7 ± 99.6 (42) ^A	71.4 ± 17.3 (39)	22.2 ± 49.8 (42)	25.8 ± 19.2 (39)	24.6 ± 17.8 (34)
Females (deep) ^b	4.8 ± 2.03 (12) ^B	3.4 ± 2.00 (24) ^{A,B}	203.3 ± 76.1 (24) ^B	64.2 ± 21.9 (12)	15.0 ± 15.0 (13)	67.2 ± 145.2 (23)	30.1 ± 38.0 (57)
Females (shallow) ^c	2.2 ± 1.11 (7) ^{A,B}	2.7 ± 1.95 (15) ^B	114.7 ± 102.8 (15) ^{A,B}	62.4 ± 26.5 (7)	13.8 ± 11.4 (7)	24.3 ± 33.0 (14)	25.6 ± 18.6 (25)
F	5.5	8.4	4.6	1.0	0.2	2.1	0.6
P	0.007	<0.001	0.01	0.50	0.80	0.13	0.66

^a Within columns, values with same letter in superscript are significantly different (post-hoc test; *P* < 0.05).

^b Deep-diving females.

^c Shallow-diving females.

DISCUSSION

Effect of instruments.—Activity-recording devices are very powerful tools for the study of behavior. However, recording devices potentially can affect the behavior of flying or swimming animals. The mass load of the device increases the cost of flight (Caccamise and Hedin 1985), and the drag effect can reduce swimming speed or increase the cost of transport in water (Wilson et al. 1986, Boyd et al. 1997, Butler and Jones 1997). Because female King Cormorants are 16% lighter than males, the effect of data loggers could be greater for females than for males. However, differences between control and logger-equipped birds were not significant, so we conclude that data loggers had little effect on the behavior of instrumented birds.

Body mass and physiological constraints.—The deeper dive depths of male King Cormorants may be related to their larger body mass. In general, larger species can dive longer because of the larger oxygen capacity of their bodies (Kooyman 1989). Heavier cormorant species (range 0.6 to 3.5 kg) have longer dive durations (Cooper 1986), and heavier alcid (0.16 to 0.93 kg) and penguin (1.2 to 22 kg) species attain greater maximum dive depths (Burger 1991) than their respective smaller counterparts. However, intraspecific variation in body mass is much smaller than interspecific variation. Nonetheless, male South Georgian Shags (14% heavier than females) dive longer than females (Wanless et al. 1995), and male Japanese Cormorants (*P. capillatus*; 26% heavier than females) dive deeper and longer than females (Watanuki et al. 1996). For King Cormorants, however, dive duration of males and deep-diving females did not differ, although the former were 16% heavier than the latter. Moreover, large individual variation in dive depth and duration occurred among females, although the values were independent of body mass (Table 1, Fig. 5). Thus, body mass does not seem to be an important factor affecting sexual and individual variation in dive depth and duration of King Cormorants.

Body mass is thought to be a major factor affecting the aerobic dive limit (ADL), which is defined as the maximum breath-hold that is possible without an increase in the concentration of lactic acid in the blood during or after a

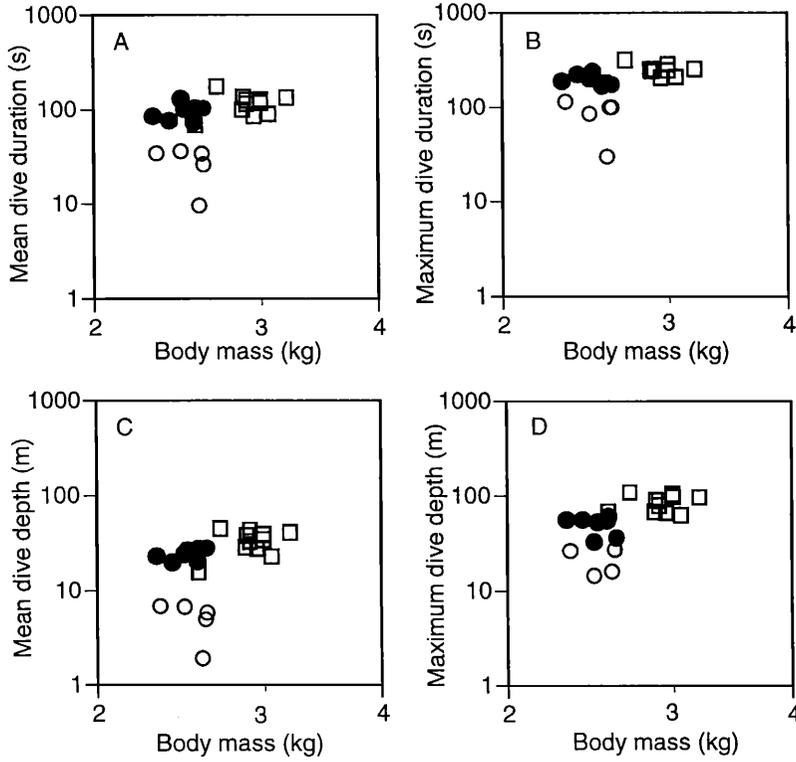


FIG. 5. Relationship between body mass and (A) mean dive duration, (B) maximum dive duration, (C) mean dive depth, and (D) maximum dive depth for male (open square), deep-diving female (closed circle), and shallow-diving female (open circle) King Cormorants.

dive (Kooyman et al. 1983). Calculated aerobic dive limits (cADL) were determined from data on metabolic rates and oxygen stores during diving (Boyd and Croxall 1996, Butler and Jones 1997). For South Georgian Shags, cADL was estimated from the field metabolic rate ($FMR = 42 \text{ mL O}_2 \text{ min}^{-1} \text{ kg}^{-1}$), four times the basal metabolic rate, and available oxygen stores ($46 \text{ mL O}_2 \text{ kg}^{-1}$) to be 66 s (Boyd and Croxall 1996). However, the mean heart rate of South Georgian Shags during diving was not significantly different from the resting value (Bevan et al. 1997). Because heart rate is a good indicator of oxygen consumption (Bevan et al. 1994, 1995), metabolic rate during diving is assumed to be similar to resting metabolic rate ($17.33 \text{ mL O}_2 \text{ min}^{-1} \text{ kg}^{-1}$; Bevan et al. 1997). Using this value, the estimated cADL for King Cormorants was 159 s, which is much longer than the value estimated for South Georgian Shags. Dive durations exceeded this cADL for

19% of male, 6%, of deep-diving female, and 0% of shallow-diving female King Cormorants.

When Weddell seals (*Leptonychotes weddellii*) make anaerobic dives, surface time or recovery time increases exponentially with dive duration, presumably so that lactic acid (which accumulates in the anaerobic phase) can be metabolized (Kooyman 1989). Exponential rises in surface time also have been observed in Thick-billed Murres (*Uria lomvia*) and Emperor Penguins (*Aptenodytes forsteri*) when they dived longer than 2.5 min and 8 min, respectively (Croll et al. 1992, Kooyman and Kooyman 1995). These observed ADLs were longer than their cADLs (0.8 min for Thick-billed Murres and 5 min for Emperor Penguins), suggesting that cADLs were underestimated. For King Cormorants, an exponential rise in surface time was not observed, and the dependence of dive duration on subsequent surface times was weak (Fig. 3).

If birds did not clear the oxygen or lactic acid debt after each dive, but did so within bouts or after bouts, an exponential increase would be expected in (1) mean surface interval against mean dive duration within a bout, or (2) interbout interval against the preceding bout duration. For King Cormorants, the effects of mean dive duration on mean surface time within a bout were stronger than those of dive duration on the preceding or subsequent surface time, although the interbout interval was not correlated with the preceding bout duration (Fig. 3). Moreover, there was no cumulative effect on dive duration or surface time, even in a long bout. These data suggest that King Cormorants did not recover oxygen stores or clear their lactate accumulation after each single dive but compensated within a bout, or that they dived aerobically.

Decreased metabolic rate during diving could enable King Cormorants to dive aerobically longer than the cADL. Abdominal or stomach temperatures in King Penguins (*Aptenodytes patagonicus*) and King Cormorants declined during diving (Culik et al. 1996, Kato et al. 1996a, Handrich et al. 1997), and heart rate of Emperor Penguins decreased during diving (Kooyman et al. 1992). Heart rate and body core temperature of South Georgian Shags also declined during diving, and heart rate declined more when they dived longer and deeper (Bevan et al. 1997). These observations suggest that metabolic rate decreases during diving and that birds can maintain the aerobic metabolic pathway while submerged. Hence, cADL of King Cormorants was probably still underestimated, and birds made fewer anaerobic dives than expected.

Foraging efficiency.—King Cormorants descended and ascended rapidly between the surface and a certain depth and spent some time at that depth (bottom time). Because cormorants are benthic feeders, bottom time is the potential feeding time, and the depth to which they dive is the foraging depth. Because benthic feeders can obtain food only when they are on the seabed, we would expect cormorants to maximize the proportion of bottom time within a dive cycle (=dive duration + surface time), which is defined as foraging efficiency (Wilson and Wilson 1988, Houston and Carbone 1992). On average, foraging efficiency of King Cormorants was higher for shallow divers than for

deep divers (Table 1). Foraging efficiency is higher for shallow dives because travel times and surface times increase with increasing dive depths (Fig. 3). Even though bottom time, descent rate, and ascent rate also increased with dive depth, travel cost and recovery time seemed to be relatively high for deep dives. However, birds made deep dives despite the associated low foraging efficiency. We suggest that shallow dives are not energetically efficient depending on prey distribution, even if foraging efficiency is higher for shallow dives in terms of time allocation. Optimal foraging depth would depend on prey distribution and size of the diver (Mori 1998).

Foraging behavior and diet.—Male and female King Cormorants segregated their foraging time in the afternoon and morning, respectively (Fig. 4). Sexually distinct activity rhythms are known for all taxa thus far studied in the blue-eyed shag group (Bernstein and Maxson 1984, Wanless et al. 1995, Green and Williams 1997). Nonbreeding Heard Island Shags (*P. nivalis*) dived in the morning and afternoon, whereas breeding pairs showed sexually distinct foraging patterns (Green and Williams 1997). If feeding time diverged, any male that did not follow the pattern and foraged with females would lose his territory, nest, eggs, or chicks (Bernstein and Maxson 1984). Therefore, obligatory nest guarding perhaps is an important factor that selects for sexually distinct foraging patterns.

Food composition differed between male and female King Cormorants. Major food items were two species of inshore demersal fish. Males fed mainly on larger-sized *Paranotothenia magellanica*, and females fed mainly on *P. magellanica* and smaller-sized *Harpagifer georgianus* (Kato et al. 1996b). In Great Cormorants (*P. carbo*), males have a larger bill than females and take larger fish (Koffijberg and van Eerden 1995). Male King Cormorants have a larger bill than females (Marchant and Higgins 1993), and they might be able to feed on larger fish more efficiently than do females.

Individual variation in dive depth among female King Cormorants could be related to variation in diet. Although we did not examine individual variation in diet in King Cormorants, sexual differences in diet have been reported (Kato et al. 1996b). No data exist for depth preferences of prey fish. From the correspondence

between diving depth and food size observed between sexes, however, shallow-diving females might feed more on small fish than do deep-diving females, which could lead to differences in the species composition of diets. Gentoo Penguins (*Pygoscelis papua*) at South Georgia fed on small krill only during shallower dives and on large fish during deeper dives (Croxall et al. 1988). Similarly, female northern fur seals (*Callorhinus ursinus*) exhibited two distinct diving patterns that apparently were specific to prey type (Costa 1988, Gentry et al. 1986). These observations suggest that deep diving is only economical when feeding on large prey, and that predation on small prey is limited to shallow depths (Costa 1991).

Male, deep-diving female, and shallow-diving female King Cormorants could forage in different sites. Sexual differences in foraging sites have been reported in Wandering Albatrosses (*Diomedea exulans*; Weimerskirch et al. 1993) and northern elephant seals (*Mirounga angustirostris*; Stewart and DeLong 1995). Time from departure to the first dive and time from the last dive to arrival, representing distance from the colony to the foraging site, did not differ between males, deep-diving females, and shallow-diving females (Table 3). However, dive depth, representing the water depth of the foraging site, was variable. The small variation in dive depth within bouts and the large variation between bouts suggested that individuals foraged on a prey patch during a bout and then changed foraging sites between bouts. The longer bout duration of males suggested that they tended to select prey patches of higher quality than did females, even if they were at deeper sites. Because foraging sites and diet seem to differ among individuals, prey availability could vary with time of day for individuals. This could be the reason why females foraged in the morning and males in the afternoon.

Foraging effort and meal delivery.—As brood mass increased, females increased their meal delivery rates and both males and females increased their proportion of time at sea. On the other hand, the number of dives per day, total dive time, and total bottom time did not depend on brood mass. These results imply that adults fed more efficiently or allocated more food for their chicks than to themselves when food requirements of their chicks increased. In-

creased time at sea might reflect increased foraging effort to find a better prey patch.

Daily total dive time and daily total bottom time did not differ among males, deep-diving females, and shallow-diving females because shallow-diving females made more dives per day than the others (Table 1). Although females fed on smaller fish than males, mass of food load did not differ between males and females (Kato et al. 1996b). Males and females seemed to deliver the same amount of food to their chicks at the same rate (Table 2). Therefore, provisioning of chicks did not differ between males and females, suggesting that prey capture rate (amount of prey/bottom time or dive time) was the same for both sexes.

In conclusion, male King Cormorants dived deeper and longer than females, and females showed large individual variation in foraging independent of body mass. Despite the variety of foraging strategies, foraging effort and food provisioning of chicks did not differ between the sexes because shallow-diving females compensated for their shallow and short dives by diving more frequently. We suggest that the foraging behavior of King Cormorants is more strongly affected by ecological factors such as prey availability than by physiological constraints.

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