

FORAGING BEHAVIOUR AND DIET OF THE GUANAY CORMORANT

C. B. ZAVALAGA* and R. PAREDES†

Maximum dive depths, timing and duration of foraging trips and diet of the guanay cormorant *Phalacrocorax bougainvillii* were investigated in January/February 1995 and February 1996 at the headland of Punta San Juan, Peru. Results from 27 birds engaged in chick rearing showed that the mean maximum dive depth was 33.9 ± 2.6 m, with a deepest dive of 74 m. A large flock of non-breeding guanay cormorants (about 140 000 birds) foraged only during daylight, with modal departure and arrival times of 09:00 and 16:00 respectively. Arrival times were more variable than departure times. Cormorants flew almost exclusively parallel to the coast (92% of cases), with feeding frenzies observed mainly within 1–3 km of the coast. Duration of foraging trips averaged 6.2 h ($CV = 34\%$), and increased significantly throughout the season. There were interannual differences in diet composition, but generally Peruvian silverside *Odonthestes regia regia*, Peruvian anchovy *Engraulis ringens* and mote sculpin *Normanichthys crockeri* were the main food delivered to cormorant chicks, accounting for 45, 29 and 16% of the overall number of items respectively. Maximum dive depths suggest that guanay cormorants not only feed just below the surface, but that they can also exploit much of the water column. Short-term variations in the timing and duration of foraging trips of guanay cormorants probably reflect the unpredictable and patchy distribution of their main prey.

Of the 19 species of seabirds nesting off the coast of Peru, the guanay cormorant *Phalacrocorax bougainvillii*, the Peruvian booby *Sula variegata* and the Peruvian pelican *Pelecanus thagus*, hereafter referred to as guano birds, have been the most abundant (Duffy *et al.* 1984). From historical times the guanay cormorant has been the dominant avian species in the ecosystem of the Peruvian Coastal Current, in terms of numbers and consumption of marine resources (Murphy 1936, Vogt 1942, Hutchinson 1950). Guanay cormorants inhabit the western coast of South America from Isla Lobos de Tierra ($6^{\circ}28'S$), Peru, south to Isla Mocha ($38^{\circ}30'S$) in Chile (Murphy 1936). Small breeding colonies have been reported also in Argentina (Erize 1972, Punta 1989). The population in Peru has been highly variable during this century as a result of *El Niño* events, human exploitation and competition with fisheries for food (Duffy 1994). It ranged from <4 million birds during the period 1909–20 (Duffy 1983a) to about 21 million birds in 1954/55 on the northern-central coast of Peru (Tovar *et al.* 1987). In 1996, the population in the same region was estimated at 3.7 million individuals (Jahncke 1998).

In spite of the fact that guanay cormorants are considered a valuable and abundant seabird, information about their foraging and breeding ecology is scarce. Studies on their dive capabilities have relied mainly on indirect sources of data, such as diving time (Duffy 1983b) or the habitat used by their prey (Jordán 1967, Vogt 1942). Murphy (1936) pointed out that

guanay cormorants feed only on surface organisms and not on benthic prey. Duration of submergence when feeding has been estimated to be between 10 and 30 seconds (Duffy 1983b), suggesting that dives are shallow. Muck and Pauly (1987) proposed a model of monthly consumption of Peruvian anchovy *Engraulis ringens* by guano birds, which assumed that guanay cormorants cannot dive deeper than 15 m. Conversely, it has been stated that diving depths of these birds can exceed 12 m (Jordán 1967) or 15 m (Duffy 1980), but depths to which they dive have not been measured.

Based on analysis of otoliths in regurgitated pellets, it has been shown that guanay cormorants feed mainly on Peruvian anchovy (Coker 1919, Murphy 1936, Jordán 1967, Jahncke and Goya 1997), a small pelagic schooling fish that supported the world's largest fishery in the late 1970s (Idyll 1973). However, these data were obtained mainly from the northern coast of Peru, where anchovy shoals are more densely concentrated than in other areas (Pauly and Tsukayama 1987). Information on the diet of guanay cormorants in southern Peru is scarce.

In this study, capillary-tube depth gauges were used to obtain the first data on the maximum dive depth attained by breeding guanay cormorants at Punta San Juan, a guano-bird headland in southern Peru. Also reported is the timing and duration of foraging trips of non-breeding birds and prey composition of meals fed to chicks.

* Av. Guardia Chalaca 1333, Callao, Peru. E-mail: czav@telematic.edu.pe

† Calle Micaela Bastidas 158–160, Lima 32, Peru. E-mail: gaviota@datos.limaperu.net

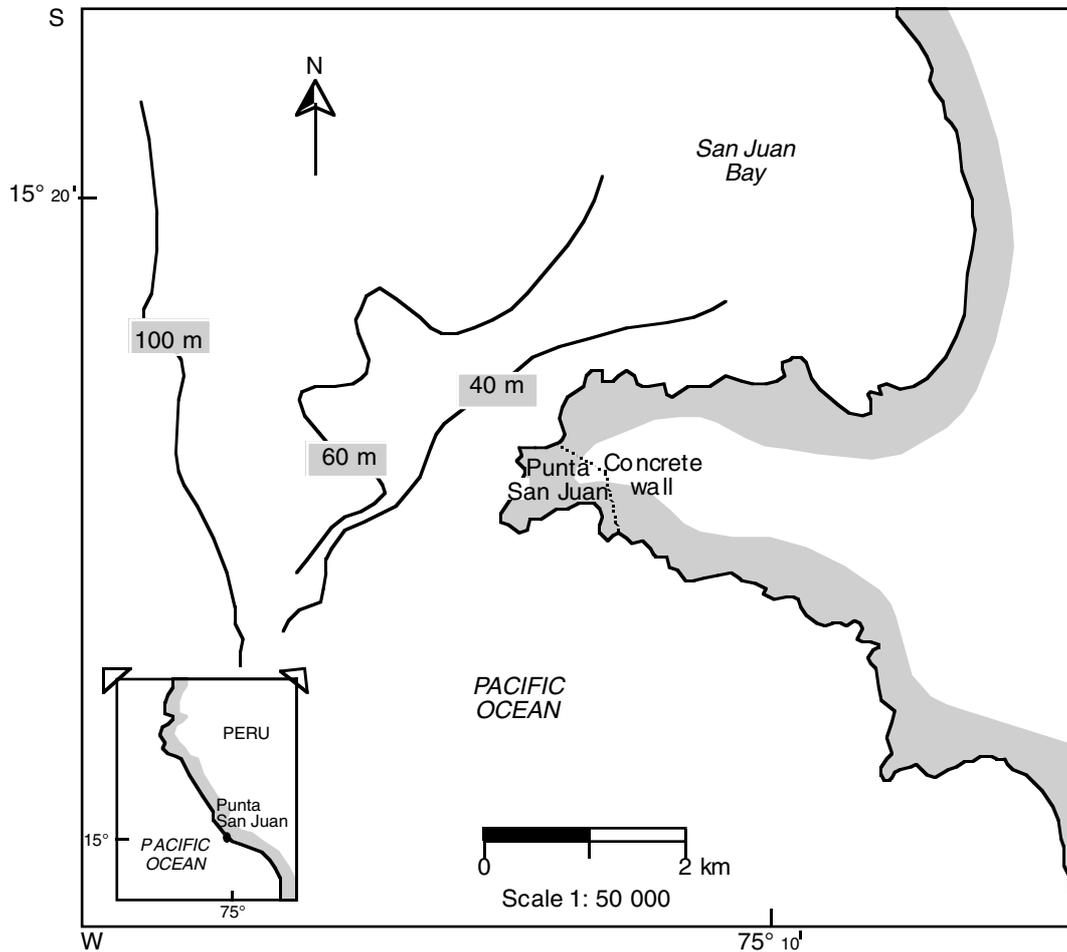


Fig. 1: Map of Punta San Juan showing the bathymetry

MATERIAL AND METHODS

The study was carried out at Punta San Juan ($15^{\circ}22'S$, $75^{\circ}12'W$), a 54-ha guano-bird headland located in southern Peru (Fig. 1). The population of adult guanay cormorants within Punta San Juan was estimated to be 178 224 birds in December 1994 and 547 508 in February 1996, but there were only 17 663 and 33 352 active nests respectively (CBZ and RP unpublished data). Mean sea surface temperature at Punta San Juan in January and February of 1995 and 1996 averaged 17.5 and $14.9^{\circ}C$ respectively. These temperatures were $+1.6^{\circ}C$ and $-1.1^{\circ}C$ from the average for these months between 1958 and 1993 (P. Majluf, Wildlife Conservation Society, unpublished data).

Therefore, it was assumed that oceanographic conditions during the study were typical for that period.

Depth gauges

Maximum-depth recorders were fitted on 54 adult guanay cormorants in January/February 1995 and February 1996, when they were brooding small chicks (2–3 weeks old). These devices recorded the single deepest depth attained by each bird (Burger and Wilson 1988). Data were collected at peripheral nests of a discrete breeding group composed of approximately 1 500 pairs. Birds were captured and recaptured at their nests by hand or by hooking them around the foot with a pole. Devices were attached directly to

the contour feathers of the central back using Epoxy-resin (Devcon 5-minute epoxy), and were retrieved one day later. To minimize disturbance in the colony, no attempt was made to recapture birds on subsequent days. Devices attachment took approximately 10 minutes from capture to release.

Manufacture and calibration of the devices were similar to those described previously by Zavalaga and Jahncke (1997). However, the gauges deployed in this study were larger, with a total length of 10 cm.

The maximum depth attained was calculated by the equation:

$$D_{max} = 10.08[(L_s/L_d) - 1] \quad ,$$

where D_{max} is the maximum depth in metres, 10.08 is the column of seawater (m) equivalent to 1 atmosphere of pressure, L_s is the total length of the tube and L_d is the length of the tube with undissolved indicator (Burger and Wilson 1988). After recovery of the recorders, the length of the tube with indicator was measured to the nearest 0.1 mm using calipers. Tubes with water droplets in the lumen were discarded.

The maximum depths recorded from the gauges overestimated real depths by an average of <8% over the range of depths investigated. Estimated depth was corrected using the equation:

$$\text{Real depth} = 3.12 + 0.8 \times \text{estimated depth} \quad (\text{Zavalaga and Jahncke 1997}).$$

All means are expressed as $\pm 1 SE$.

Foraging trips

Individual foraging trips of breeders were difficult to assess because of the high density of breeding pairs in the colony (about 3 nests·m⁻²). Also, peripheral nests were usually completely surrounded by non-breeding birds in the late afternoon, so that dye-marked birds could not be resighted. However, attempts were made to estimate the duration of foraging trips by monitoring a large non-breeding flock (about 140 000 birds), which showed regular times of departure and arrival. The number of birds within this group remained fairly constant throughout the study period and could be monitored from a distance without disturbing the birds.

Observations of foraging patterns were undertaken on 26 days between November 1994 and March 1995. The activity of the flock was monitored at hourly intervals between 06:00 and 18:00 from a high spot 500 m away. During the study period, sunrise was between 05:30 and 06:00 and sunset between 18:30 and 19:00. Departures and arrivals were defined as the time when about 50% of the birds had left from

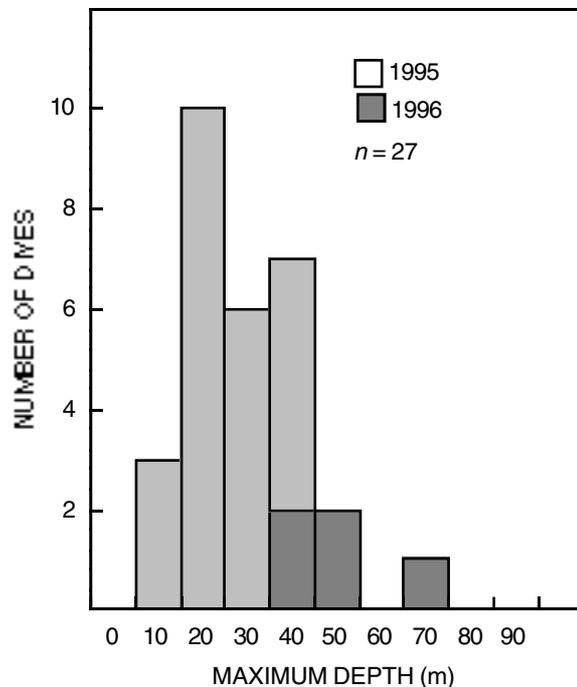


Fig. 2: Frequency distribution of the maximum dive depths of breeding guanay cormorants at Punta San Juan

or arrived at the colony respectively. A foraging trip of the flock was considered to be the time elapsed between departure and arrival. It took about two hours for all birds to leave or arrive at the colony. To minimize bias in the analysis, only those days in which all birds left the colony were included. The direction in which the birds flew after departure was observed and recorded for three 60° sectors: south, north and west. Opportunistic observations of feeding frenzies were done from land around Punta San Juan throughout the study period. Distances from shore were estimated by eye, using small islets and scaled maps as references.

Diet

In all, 93 stomach contents were obtained from regurgitations of guanay cormorant chicks of different age-classes between 20 January and 17 February 1995 and between 14 January and 4 February 1996. The regurgitations were produced spontaneously when the chicks were handled during the course of other fieldwork. Most of the vomits were undigested, so each sample was easily sorted into different prey types.

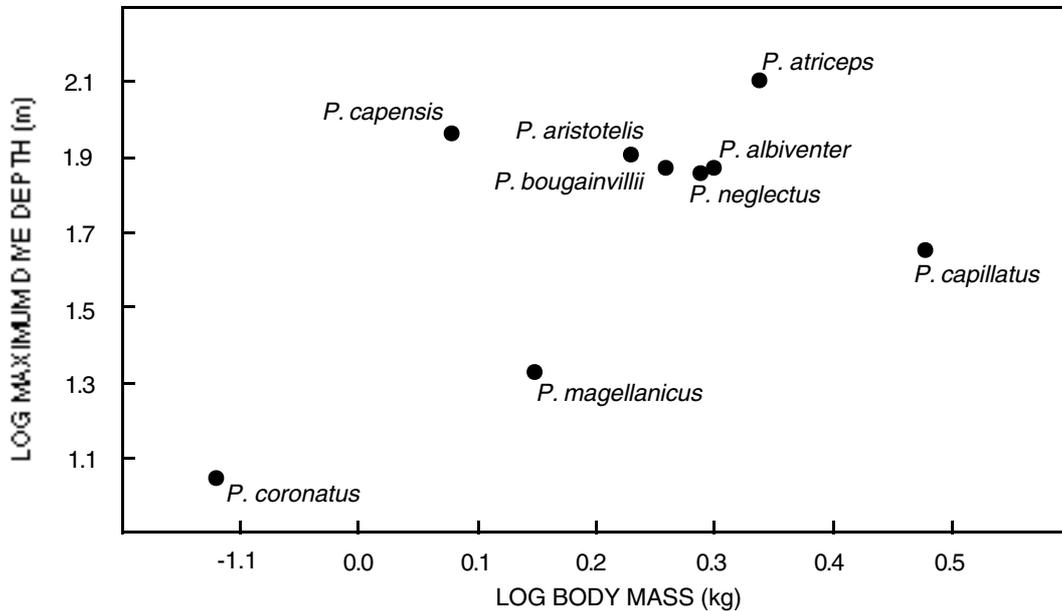


Fig. 3: Allometric relationship between body mass and maximum dive depth (m) for nine species of cormorants. Data are from maximum depth gauges used in several studies (Burger 1991). The maximum dive depth for Japanese cormorants *Phalacrocorax capillatus* was taken from Watanuki *et al.* (1996). Data for Imperial cormorants *Phalacrocorax albiventer* and rock shags *Phalacrocorax magellanicus* were provided by G. Punta (unpublished data)

Numbers of each prey type were counted. Mass of different prey types was recorded for 26 samples during the 1994/95 season. Total length of intact fish was measured to the nearest 1 mm.

RESULTS

Maximum dive depths

Of 54 depth gauges deployed, 27 were recovered one day after attachment. Mean maximum dive depth was 33.9 ± 2.6 m ($n = 27$), with 80% of the maximum dives between 20 and 50 m (Fig. 2). The shallowest maximum dive depth was 14 m, and the deepest was 74 m.

Maximum dive depths were shallower in January 1995 (mean = 26.1 ± 1.8 m, $n = 13$) than in February 1995 (mean = 33.5 ± 3.4 m, $n = 9$), but these differences were not significant (Mann-Whitney $U = 34$, $p = 0.10$). However, guanay cormorants dived significantly deeper in February 1996 (mean = 55.0 ± 5.0 m, $n = 5$) than in February 1995 (Mann-Whitney $U = 2.0$,

$p = 0.006$).

There was no allometric correlation between the maximum dive depth attained by nine species of cormorants and their body mass (Spearman Rank Correlation Coefficient $r_s = 0.251$, $p > 0.05$, Fig. 3).

Timing, duration and location of foraging trips

Guanay cormorants foraged only during daylight. The flock was approached occasionally at night to investigate flying activity, but the cormorants were always resting. Modal times of departure and arrival were 09:00 (between 06:30 and 10:00, $n = 26$) and 16:00 (between 11:00 and 18:00, $n = 26$) respectively. Arrivals were more variable ($CV = 13.5\%$) than departures ($CV = 8.8\%$). Duration of foraging trips averaged 6.2 h ($CV = 34\%$) and increased significantly throughout the season (Spearman Rank Correlation Coefficient $r_s = 0.66$, $p < 0.01$, $n = 26$, Fig. 4). On 92% of the trips ($n = 26$), cormorants left the colony parallel to the coast (south = 67%, north = 25%), whereas they travelled west on 8% of occasions. Some 10 out of 15 feeding frenzies observed were

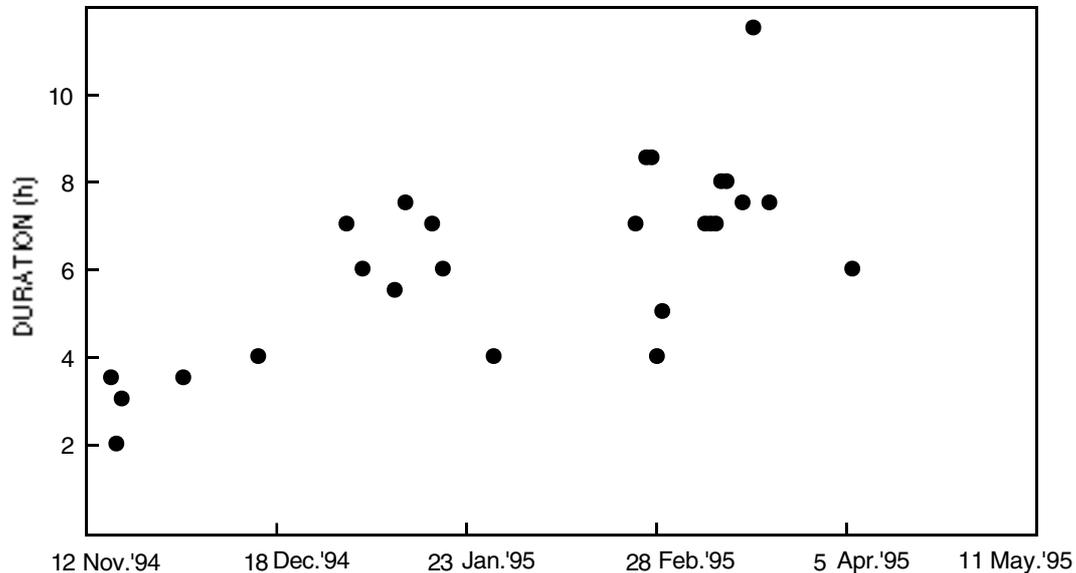


Fig. 4: Relationship between date and duration of foraging trips of a large flock (about 140 000 birds) of non-breeding guanay cormorants at Punta San Juan

within 1–3 km of the coast, with the remainder 4–6 km offshore.

Diet

Six species of fish were identified in the 563 prey items examined during the study. No attempt was made to calculate mean mass of meals, because many of the regurgitations may have been incomplete after collection. Relative abundance (%) of anchovy and Peruvian silverside *Odonthestes regia regia* in a sample of 26 stomach contents was the same, whether ex-

pressed by number or by mass (Wilcoxon Signed Rank Test, anchovy: $W = 3.0$, $p = 0.81$; silverside: $W = -9.0$, $p = 0.44$). Because of this similarity, and because mass of prey was not recorded for most of the samples, diet composition is expressed only as percentage by number. The relative contributions of prey species to the diet and the mean sizes of fish eaten are shown in Table I. Silverside, anchovy and mote sculpins *Normanichthys crockeri* were the most commonly eaten species, accounting for more than 90% of prey items. Prey composition varied between years. In summer 1995, anchovy were the most common prey found in regurgitations (65%), followed by silver-

Table I: Percentage contribution by number, mean total length and habitat of prey delivered to guanay cormorant chicks at Punta San Juan, 20 January–17 February 1995 ($n = 39$) and 14 January–4 February 1996 ($n = 54$)

Prey		Habitat	% by number			Total length (cm)	
Common name	Species		1995	1996	1995 and 1996	Mean \pm 1SE	n
Peruvian silverside	<i>Odonthestes regia regia</i>	Pelagic-inshore	23	60	45	12.7 \pm 0.5	28
Peruvian anchovy	<i>Engraulis ringens</i>	Pelagic-inshore	65	2	29	12.6 \pm 0.3	45
Mote sculpin	<i>Normanichthys crockeri</i>	Pelagic-inshore	5	24	16	6.0 \pm 0.01	43
South Pacific saury	<i>Scomberesox saurus</i>	Pelagic-inshore	0	11	6	25	1
Southern jack mackerel	<i>Trachurus picturatus</i>	Pelagic-inshore	7	0	3	19	1
Cabinza grunt	<i>Isacia conceptionis</i>	Benthic-inshore	0	2	1	–	–

side (23%). In February 1996, the silverside and mote sculpin were the main fish delivered to chicks (60% and 24% respectively), with anchovy constituting only 2% of prey items.

DISCUSSION

Maximum dive depth

The deepest dive attained by guanay cormorants brooding chicks at Punta San Juan was 74 m, deeper than has been previously suggested for the species (Murphy 1936, Muck and Pauly 1987). Off Punta San Juan, the 40- and 60-m isobaths are 1 and 3 km from the coast respectively (Fig. 1), where guanay cormorants were generally foraging. Because more than 80% of guanay cormorants attained depths of between 20 and 50 m, it is suggested that they not only feed near the surface but that they are also capable of foraging deeper in the water column, approaching the seabed at least once in pursuit of their prey. Mesopelagic and benthic fish have been found in their diet at Punta San Juan (Tovar and Guillén 1989) and elsewhere along the Peruvian coast (Jahncke and Goya 1997), suggesting that they occasionally feed near or on the seabed.

There is a strong allometric correlation between the maximum depth of dive of wing-propelled seabirds and their body mass (Piatt and Nettleship 1985, Burger 1991). However, when such a trend was examined for nine species of foot-propelled cormorants, no significant relationship was found (Fig. 3). These results suggest that factors other than body mass, such as the distribution and type of prey (Burger 1991), use of habitat by birds (Wilson and Wilson 1988, Punta *et al.* 1993), water visibility (Wilson *et al.* 1993) and the depth and topography of the seabed (Scolaro and Suburo 1991) may also constrain the depth to which cormorants dive.

It has been suggested that temporal variation in the maximum dive depths of wing-propelled divers, such as the Adelie penguin *Pygoscelis adeliae* (Whitehead 1989) and common diving-petrel *Pelecanoides urinatrix* (Chastel 1994) may reflect changes in the relative abundance or the vertical distribution of their main prey. In 1995, guanay cormorants were feeding mainly on anchovy (65%), whereas in 1996 the dietary contribution of anchovy was only 2%. The shallower dives recorded in February 1995 relative to those in February 1996 suggest that anchovy shoals were deeper and less available to cormorants in 1996. Alternatively, the dominant prey item in 1996 (silverside) may have been deeper in the water column.

Guanay cormorants feed on a wide range of fish species (Tovar and Galarza 1984, Jahncke and Goya 1997). In interpreting the present results, it should be borne in mind that maximum dive gauges record only the deepest dive attained during one or more foraging trips. Among pelagic and midwater foragers, these might represent rare exploratory dives more than modal foraging depths (Burger and Wilson 1988, Lishman and Croxall 1983).

Timing and duration of foraging trips

Duration of foraging trips of non-breeding birds recorded in this study was highly variable ($CV = 34\%$) and longer than those reported for individual breeders in other colonies. Duffy (1983c) noted that breeding guanay cormorants usually spent <2 h foraging around Isla Mazorca in northern Peru. Vogt (1942) postulated that trips shorter than 6 h may indicate a high availability of food and cormorants could forage more than once a day under such conditions. Because the duration and frequency of foraging trips could be different between breeding and non-breeding birds, the present results may not be comparable with those of breeders.

Short-term variation in the timing and duration of foraging trips of guanay cormorants may reflect the spatial distribution of their prey. For example, Peruvian anchovy occur in widely scattered shoals of different sizes (Mathisen 1989). During the day, they form compact shoals, whereas at night they are more dispersed (Jordán 1971). If guanay cormorants feed on large and spatially predictable fish shoals, the birds would be expected to travel almost the same distance every day, resulting in low variability in the timing and duration of foraging trips. In contrast, if shoals are spatially unpredictable and in patches, the birds would travel variable distances, with a concomitant higher variability of duration of feeding trips and a less predictable time of returning to their roosting sites. The latter seems to be the case. At Punta San Juan, guanay cormorants fed exclusively during daylight, with departure and arrival times between 06:30 and 10:00, and 11:00 and 18:00 respectively. Arrival times were more variable than departures. Vogt (1942) found that guanay cormorants foraged mostly during daylight, with departure times ranging from 06:00 to 10:30. Jordán (1959) found that departure times of cormorants were between 06:30 and 10:30, with a peak at 09:30.

Foraging trips of non-breeders tended to increase through the season, from about 2 h in November 1994 to 8 h in March 1995 (Fig. 4), suggesting that food could be more dispersed and difficult to find late in the season. Because the duration of feeding trips by

flocks of non-breeding birds is not dependent on the stage of the breeding cycle, as found in other species of seabirds (Wilson and Wilson 1990), it may be a good indicator of the horizontal distribution of prey around their roosting sites.

Diet

More than 90% of the prey delivered to guanay cormorant chicks were small, epipelagic schooling fish: silverside, anchovy and mote sculpin (Table I). Although some 30 different species of fish, as well as squid, crustaceans and molluscs have been found in the diet of guanay cormorant (Guillén 1993, Jahncke and Goya 1997), anchovy and silverside appear to be the most important prey of guanay cormorants along the Peruvian coast (Tovar and Galarza 1984, Tovar and Guillén 1989, Jahncke and Goya 1997).

The switching of prey by guanay cormorants at Punta San Juan observed during this study likely reflects changes in the relative abundance and distribution of prey. During summer 1994/95, when cormorants fed mainly on anchovy, that prey was readily available around Punta San Juan (Segura *et al.* 1995). Anchovy shoals were predominantly inshore (up to 30 miles from coast) and shallow (0–20 m deep), with higher biomass and densities around Punta San Juan than elsewhere (Cárdenas *et al.* 1996). Conversely, during summer 1995/96 summer, when anchovy were scarce in the diet, anchovy shoals were not found around Punta San Juan (Segura *et al.* 1996).

Seasonal and interannual changes in the dietary contribution of prey of guanay cormorants at Punta San Juan has been recorded by Tovar and Guillén (1989) and Jahncke and Goya (1997). High interannual variability in oceanographic parameters and marine productivity are major features of the marine ecosystem off the coast of Peru, even during so-called "normal" years (Barber *et al.* 1985, Bakun 1987). Guanay cormorants adapt to this variability by foraging over a wide range of the water column, enabling them to exploit different prey types.

ACKNOWLEDGEMENTS

We are grateful to our colleagues Messrs A. Bertolero, A. Black, D. Blake, G. Battistini and A. Valdéz, for help with the fieldwork. We thank Dr G. E. Punta (Director de Intereses Marítimos, Chubut), who kindly provided unpublished diving information on Imperial cormorants and rock shags. Dr R. J. M. Crawford of Marine and Coastal Management, Cape Town, provided valuable comments on an early draft of this manuscript.

We thank the División de Fertilizantes Pesca-Peru for permission to work at Punta San Juan and for providing accommodation. The work was partially supported by the Wildlife Conservation Society of USA.

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