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This issue of SPN:

The major articles in this issue, with the exception of "Nesting Sites for Spheniscus Penguins," are from papers presented at the Spheniscus Workshop held at the AAZPA Regional Conference in Sacramento, California, in March 1990. Other papers presented at that workshop were included in the November, 1990 SPN, and it was intended to include all remaining papers in this issue. Unfortunate realities of printing costs, however, forced a change in plan (see below for information on contributing toward production costs of this publication). Papers remaining, for our next issue, are: "Avian Malaria," "Incubation Behavior Patterns in Adelies," "Molt Patterns of Black-footed Penguins," and 'Diet, Feeding Regimen, and Growth Rates in Hand-reared Magellanic Chicks.' Thanks to the authors and to the American Association of Zoological Parks and Aquariums, for permission to reprint these papers.

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Field Studies of *Spheniscus* Penguins

David Cameron Duffy

The popular image of penguins is one of ice. However, penguins of the genus *Spheniscus* rarely if ever see ice and instead inhabit areas more tropical than polar. This has been both boon and bane. The *Spheniscus* penguins have taken the brunt of human exploitation, while until recently being more or less ignored as research subjects compared to polar penguins. Human exploitation and research neglect have now diminished, although much remains to be done concerning both conservation and research.

What follows is a selective overview, but the papers cited will provide access to the rest of the literature on each species. I would like to note that most of what we know is mostly the result of work by a very few people: Boersma on Galapagos Penguins; Scolaro on Magellanic Penguins; Araya and Hays on Humboldt Penguins; and Cooper, Rand, Randall, and Wilson on African Penguins, presently the best known of the species.

**Taxonomy**

There are currently believed to be four species of *Spheniscus* penguin: the Humboldt *Spheniscus humboldti*, Galapagos *Spheniscus mendiculus*, Magellanic *Spheniscus magellanicus*, and the African, Black-footed, or Jackass *Spheniscus demersus*, all with a very similar morphology (Livezey, 1989).

I prefer African as the common name for the last species, as Jackass is also used for Magellanic and Humboldt, and Black-footed is singularly uninformative. The other three have geographic names, so why not the African Penguin? George Gaylord Simpson (1976), the godfather of fossil penguinology, made the same plea.

Given the propensity of the various species to interbreed in captivity, a few words on their evolutionary relationships are in order. Genetically, there are at present only one study, by Grant et al. (in press), on the Humboldt, Magellanic and African taxa, using electrophoretic analysis of gene frequencies. The three species are very closely related, suggesting that if they are species, rather than subspecies, they are very recent ones. The Galapagos Penguin probably evolved from a stray colonization of the islands by Humboldt Penguins, although its double-breast pattern is more similar to that of the double-banded Magellanic than of the single-banded Humboldt. Similarly, the single-banded African Penguin may have evolved from the Magellanic or vice-versa.

Occasional individuals of the African and, less frequently, the Humboldt, have double stripes, suggesting either occasional immigration and past interbreeding with Magellanic, or that a recessive gene for double-bandedness lurks in the best of birds.

**Distribution**

The *Spheniscus* penguins range to the Equator in the Pacific and stray almost to the Equator in the Atlantic (Gabon: Shelton et al. 1984), but they are cool-water specialists, associating with upwelling marine ecosystems (Murphy, 1936).

The Galapagos Penguin has an extremely restricted range, nesting only on the west side of Isla Isabela and on Isla Fernandina in the western Galapagos Islands (Harris, 1974). The Humboldt Penguin is confined to the upwelling of the Humboldt Current of the west coast of South America, nesting from northern Peru to Chiloé Island, Chile (Araya, 1983; Hays, 1983). The Magellanic Penguin nests on the Pacific coast, from central Chile, south around Cape Horn, and north on the Atlantic, to central Argentina, as well as on the Falklands and on several of Chile’s offshore islands (Murphy, 1936; Araya and Millie, 1986). The African Penguin nests from central Namibia south around the Cape of Good Hope and along the south coast of South Africa (Rand, 1960; Shelton et al. 1984).

Only the Magellanic and Humboldt overlap in breeding range, over approximately 1750km of Chilean coast (Duffy, 1987a; Duffy et al., in prep. a). Mixed pairs have been observed but not studied. We haven’t a clue as to how the species differ in their courtship and mating behavior to prevent interbreeding in the wild.

**Colony Size And Distribution**

The *Spheniscus* penguins don’t nest in colonies so much as they nest where suitable access to the sea and suitable nesting sites occur, with nesting ranging from solitary Galapagos Penguins to immense colonies of Magellanic and African penguins. The reasons for these differences need further study. The Galapagos Penguin nests in small, scattered groups (Boersma, 1977; Harcourt, 1980; Valle, 1986). Much of its range appears too cliff-bound for birds to get ashore.

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Field Studies of Spheniscus Penguins

(Boersma, 1977), a problem faced by the other species. The Humboldt Penguin in Peru nests mostly in small colonies in sea-caves on islands and the coast, and in burrows on islands where it is slightly safer from intense poaching pressure (Hays, 1983, Duffy et al., 1984a), whereas in Chile, where human disturbance is much reduced, it nests in much larger colonies on islands (Araya, 1983). The Magellanic and African Penguins nest or nested in colonies of 10,000 to 100,000+ (Scolaro and Arias de Reyna, 1984; Scolaro et al., 1980a, 1984; Shelton et al., 1984; Capurro et al., 1988). Except for several small colonies which may suffer periodic bouts of catastrophic disturbance from humans and at least once from a leopard (Panthera pardus) (pers. observ.), African Penguins nest on islands (Shelton et al., 1984). Magellanic nests on both islands and the mainland, and it remains a mystery to me why terrestrial predators have not exterminated whole colonies. Scolaro (1985) suggests that humans have reduced local populations of terrestrial predators.

Population Fluctuations and Trends

With the possible exception of the Magellanic Penguin, the Spheniscus penguins have suffered either short-term or historical population decreases. The Galapagos Penguin, apparently otherwise stable at between 3,000 and 15,000 birds (Brosset, 1963; Harris, 1977; Boersma, 1977), lost 77% of its counted population during the strong El Niño oceanographic event in 1982-1983 and subsequently experienced poor reproduction through 1984 (Valle and Coulter, 1987). More recent data have not been published. Humboldt Penguins in Peru have been in decline since the 19th century, perhaps in part because of the removal of the guano substrate they used for their burrow nests (Murphy, 1936). I suspect, however, that human exploitation for food has been and continues to be a serious, if not the principal problem (Duffy et al., 1984a). The Peruvian and Chilean combined population was estimated to be approximately 20,000 (Hays, 1983,1984) before the 1982-1983 El Niño which reduced numbers by 65% in Peru to 2,000-3,000 (Hays, 1986). Similar reductions occurred in Chile (Araya, 1984 ms; Araya and Todd, 1988). More recent data are not available.

The Magellanic Penguin, with a population on the order of a million birds or more, is increasing in Argentina, perhaps because of changes in food availability or reduction of predators (Scolaro, 1985; Boersma et al., 1990). The status of its population in Chile is unknown, although the species is common (Schlatter, 1984). The African Penguin has suffered a population crash since the turn of the century (Burger and Cooper, 1984; Shelton et al., 1984) Between 1956 and 1978, the population decreased from 230,000 to 100,000 (Burger and Cooper, 1984), but its recent dynamics have been complex, decreasing in the center of its range and increasing or remaining stable to the north and east (Frost et al., 1976a; Siegfried and Crawford, 1978; Shelton et al., 1984). These changes have been linked to changes in fish stock (Crawford and Shelton, 1978, 1981; Burger and Cooper, 1984; Crawford et al., 1985) and overfishing (Crawford and Shelton, 1978, 1981), but the mechanisms for overfishing are unclear, as penguins and fishermen don’t fish in the same areas (Broni, 1986; Wilson et al., 1988) and fishery landings bear no relation to penguin diet or growth (Duffy et al., 1987a). Breeding success for penguins at one island studied near fishing grounds was the same as that on a control island in an unfished area (La Cock et al., 1987). At present, we believe that penguins and fishermen compete during the pelagic first-year of life of the African penguin, when juveniles from decreasing colonies disperse to areas of intense fishing and have low survival rates, whereas those from stable or increasing colonies disperse to unfished areas and survive better (La Cock et al., 1987; Duffy and Cooper, 1990).

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Natural and Unnatural Mortality

Accounts of the natural predators of *Spheniscus* penguins are numerous (e.g. Galapagos Penguin: Boersma, 1977; Humboldt Penguin: Hays, 1984, 1986; Araya and Duffy, 1987; Magellanic Penguin: Boswall, 1972; Rodriguez, 1983; Scolaro, 1985, African Penguin: Cooper, 1974; Brooke and Wallett, 1976; Frost et al., 1976a; I.Randall et al., 1988). Parasites may also be important (e.g. Boersma, 1977; Randall and Bray, 1983; Duffy and Daturi, 1987), but we have almost no idea of the impact of either parasites or predators on penguins at the population level. Such studies are urgently needed.

Human exploitation ranges from poaching (Duffy et al., 1984a; Hays, 1984; Schlatter 1984) to indigenous clothing (Avery, 1985) and industrial glove production (Scolaro, 1986) to zoo exports (Hays, 1984). Exploitation of eggs (up to 500,000/year and 13 million in 30 years: Siegfried and Crawford, 1978) in South Africa caused population decreases on at least some of the islands (Frost et al., 1976a). Oiling has been especially noticeable off South Africa, on the route of much of the world's tanker traffic (Westphal and Rowan, 1971; Morant et al., 1981), but there is some disagreement over its impact. Frost et al. (1976a) estimated the oiling rate to be only 0.7-0.9%/year, but Randall et al. (1980) working farther to the east considered oiling the main cause of adult mortality. A major public effort, the South African National Foundation for the Conservation of Coastal Birds, operates a permanent rescue and cleaning operation that has been highly effective in returning birds to the wild and in educating the public about oil contamination (Randall et al., 1980; Morant et al., 1981). Oiling rates in Galapagos and Peru are apparently low, but there is considerable concern about oiling rates and resulting mortality of Magellanic Penguins in Argentina (Jehl, 1975; Perkins, 1983; Boersma et al., 1990).

Natural disasters, ranging from local heavy rains (Crawford et al., 1986; Randall et al., 1986b; Duffy et al., 1988) and anomalous cold-water events (Schumann et al., 1989) to species-wide El Niño-caused mortality (Vogt, 1942; Boersma, 1978; Boersma, 1987; Duffy et al., 1984a,b, 1988; Hays, 1986; La Cock, 1986; Valles and Coulier, 1987; Araya and Todd, 1988; Duffy, 1990), have been well documented, but again the population effects have been difficult to document because, with the exception of the Galapagos (Valle and Couler, 1987) and locally with the African (La Cock et al., 1987; La Cock and Hanel, 1987) and Magellanic (Boersma et al., 1990) penguins, long-term population or breeding data are not available. Computer models of penguin populations (e.g. Jackson et al., 1976; Scolaro, 1987b; Scolaro et al., 1981) may help assess the possible impact of natural, and unnatural, disasters, long before we have direct data (Duffy, 1990).

Nesting Biology

Breeding Seasons

Humboldt (Koepcke 1970; Castro and Ishiyama, 1985–1986) and African Penguins nest throughout most of the year, (Cooper, 1980; Randall and Randall, 1981, La Cock et al., 1987) but show strong seasonal variation which have been linked to differences in food availability (Wilson, 1985c) and nesting success (Wilson, 1985c; La Cock et al., 1987). Boersma (1977, 1978) showed that nesting by Galapagos Penguins can occur throughout the year, in response to appropriate oceanographic and food conditions. In contrast, Magellanic Penguin nesting is strongly seasonal (Scolaro, 1984a; Scolaro et al. 1980a; Boersma et al., 1990), perhaps because the southern distribution leaves too few daylight hours for foraging during the winter (Duffy et al., in prep a).

Nest site

The biggest problem for nesting *Spheniscus* penguins is the sun (Drent and Stonehouse, 1971; Frost et al., 1976b). They avoid it by nesting in burrows and sea caves or under vegetation (Murphy, 1936; Scolaro and Arias de Reyna, 1984b), or, if surface-nesting, doing so during the winter (La Cock, 1988) or when there is a strong windchill. When penguins nest on the surface, they tend to nest densely, to protect their eggs and young against aerial predators (Siegfried, 1977). Burrow nests appear more successful than surface nests (Frost et al., 1976a) which may be used when covered sites are occupied or substrates are unsuitable for burrowing because of texture or susceptibility to flooding (Scolaro, 1984; La Cock, 1988). Nest sites must also be accessible to the sea and, for surface nesters, essentially level, as penguins build only rudimentary nests (Duffy and La Cock, 1985). These habitat requirements combine to produce complex mosaics of nesting colony distributions and nest densities (e.g. Bodano et al., 1982; Scolaro and Arias de Reyna, 1984a,b; Scolaro, 1984; Scolaro et al., 1979, 1984, 1985; Duffy and La Cock, 1985; Capurro et al., 1988). These in turn complicate estimates of colony size (discussed above).

Breeding Behavior and Ecology

Breeding of the *Spheniscus* penguins appears relatively similar across species, although we lack details for the Humboldt Penguin in the wild. Boersma (1977); Scolaro (1978, 1980, 1983,1984a,b,d), Scolaro et al. (1980a); Cooper (1980), Hockey and Hallian (1981), Randall (1983), Williams and
Cooper (1984), and Wilson (1985c) provide details of various aspects of the breeding of Galapagos, Magellanic and African penguins, respectively. For the African Penguin, the normal clutch is two eggs, laid about three days apart, with an incubation period of 38 days, and both young are usually raised in about 80 days, except during poor food conditions, when the younger of the pair dies (Cooper, 1980; Williams and Cooper, 1984). For the Magellanic Penguin, the incubation period for the two-egg clutch is 38-42 days, with a two to four day period between eggs and an extremely variable growth of young to fledging (Boersma et al., 1990). The Galapagos Penguin also lays two eggs, three or four days apart, with an incubation period of approximately 38 days and young reach adult size at thirty days, "although some chicks remained in the nest until after 50 days of age" (Boersma, 1977), which is a very short fledging period compared to the other two species.

Growth

Growth of young in the field has been extensively studied in African Penguins (Cooper, 1977; Williams and Cooper, 1984; Duffy et al., 1987a). Heath and Randall (1985) examined growth of African penguins fed different diets. Boersma (1977) provided the only growth data for the Galapagos Penguin, and Scolaro (1984d) and Boersma et al. (1990) for Magellanic. No published data exist for Humboldt Penguins.

Moult

Moult takes approximately 20 days in Humboldt Penguins, 10-15 days in Galapagos Penguins, and 18 days in African Penguins, during which time the birds fast and usually do not enter the water (Boersma, 1977; Cooper, 1978). For Magellanic Penguins, moult occurs during a relatively short, fixed time of year, after breeding and prior to dispersal from the colony (Scolaro, 1984d). This fixed pattern appears to be a response to the strongly seasonal and consistent pattern of climate and food availability, not found in the environments of the other species. African and Galapagos Penguins can be found moulting throughout the year, but African Penguins exhibit a strong seasonal peak in October-November (Randall and Randall, 1981). Moult is a pre-breeding activity in Galapagos Penguins (Boersma, 1977). It occurs, although not in the same birds, both immediately before and after breeding in African Penguins (Cooper, 1978), but appears to be predominantly post-breeding (Randall and Randall, 1981). Galapagos Penguins moult twice a year (Boersma, 1977), perhaps as a response to damage to plumage by the equatorial sun. If this is the case, the similar frequency of moult should occur in Humboldt Penguins. Moult in African Penguins and Magellanic appears to be annual (Randall and Randall, 1981; Scolaro, 1984).

Moult appears to be extremely stressful, and birds may be forced to return to the water to forage before completion (Boersma, 1977), even though they lack thermal protection against the cold (Erasmus et al., 1981) and may be too slow to catch their normal prey (Wilson, 1985b).

Foraging Biology

Diet

Early diet work involved killing birds. The development of an effective stomach pump (Wilson, 1984) removed all necessity to slaughter penguins for diet studies. Problems remain, however, as diet analyses can be biased by a variety of factors, including methods of analysis, and comparisons of data can be hindered by differing methods of presentation (Duffy and Jackson, 1986). Another complication is differential digestion of prey species, which has led to studies of penguin digestive rates (Furness and Laugksch, 1983; Duffy et al., 1985a; Wilson et al., 1985; Laugksch and Duffy, 1986; Wilson et al., 1989b).

Diet reviews which summarize previous work include: African Penguin: Randall (1960); Randall and Randall (1986); Duffy et al. (1985a, 1987a,b); Humboldt: Wilson et al. (1989a); Duffy et al. (in prep. a); Galapagos: Boersma (1977) and Magellanic: Gosztonyi (1984); Scolaro and Bodano (1985). Basically, Spheniscus penguins eat a wide variety of species and sizes of prey, from 10 to 310 mm (Wilson and Wilson, 1990) but specialize on small, schooling fish, such as anchovy Engraulis spp. and sardines Sardinops.

Distribution at Sea

Measurement of distribution at sea is extremely difficult, as penguins ride low in the water and travel under water, reducing the chance of seeing them. The two traditional ways of studying them have been to measure the duration of foraging trips and to run transects at sea. In the first case, the departure and return times of penguins, especially those with small young, are measured (Boersma, 1977; Wilson, 1985a). By assuming a certain traveling speed and time spent actually foraging, a maximum range can be calculated (Wilson, 1985ab; Duffy et al., 1987a; Wilson et al., 1988). These measurements are necessarily rather crude.

In the second case, direct observation, penguins are counted on transects from moving vessels. Observations
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include distance from shore, group size, social behavior, and attendance in foraging groups (e.g. Rand, 1960; Siegfried et al., 1975; Duffy, 1983, 1989; Broni, 1986; Wilson et al., 1986b, 1988). Unfortunately, transects require strong stomachs, are extremely expensive to run, and are frequently interrupted by bad weather. The presence of a vessel may also influence penguin behavior.

More recently, methods have been developed to measure *Spheniscus* penguin foraging at sea, through remote sensing. Small measurement packages are placed on the bird (e.g. Heath, 1987; Wilson and Wilson, 1989a) and either store data until recovered or transmit them by radio. Speed, depth and distance meters store data on x-ray film, using small amounts of radioactivity to mark the film (Wilson and Bain, 1984a,b) or use a counter to store counts of propeller turns (Wilson and Achleiter, 1985). When combined with diet data from birds returning colonies, the devices allow estimates of foraging effort versus food ingested (e.g. Nagy et al., 1984).

Radio-transmitters provide continuous signals while birds are on the surface (Heath and Randall, 1989). Interruption of the signal is caused by submergence, so the device can be used to measure dive frequency and duration. Range of signal can be a problem, as penguins ride so low in the water that waves intercept signals. Also, triangulation of radio-signals and pursuit of animals with airplanes or boats is necessary for locating the birds at sea. Nevertheless, radio-transmitters can provide an abundance of detailed data which can be combined with direct, simultaneous observations of foraging situations and prey. Where telemetry is not possible, a new dead-reckoning device may provide similar data, although it requires recovery of the bird with the device (Wilson and Wilson, 1988).

A potentially serious problem with devices and methods of attaching them is the increased drag or water-resistance they can create when the penguins are diving. Drag may hamper foraging or cause birds to desert their nests (Wilson et al., 1986a), so recent devices have tended to be as small as possible. In addition, either the devices or their attachments may annoy the birds sufficiently to generate aberrant behavior. Wilson and Wilson (1989b) developed a device to count the number of pecks directed at devices, as a measure of disturbance. Finally, the disturbance caused by capturing the bird to install and remove devices may be a serious problem, especially perhaps for birds such as Humboldt Penguins in Peru, that appear much more shy than other *Spheniscus* populations (pers. observ.). Automatic injection of sedatives by remote control may reduce trauma (e.g. Wilson and Wilson, 1989c).

During the breeding season, penguins return to shore. Frequently, especially when feeding young, so they tend to be distributed at sea near their colonies. During their first year of life and, while non-breeding, penguins may be pelagic for extended periods of time (Wilson et al., 1988; Duffy and Cooper, 1990).

Foraging Behavior

Wilson and Wilson (1990) have recently reviewed *Spheniscus* foraging. They report that *Spheniscus* penguins travel at 6.8–7.4 kph underwater and at 12.3 kph while porpoising. Dives can last as long as 146 sec and reach mean maximum depths of 60+ m, although most dives are shallower. They may travel as much as 72 km per day while providing food for young.

Unfortunately, we know relatively little about actual foraging behavior, as events take place tens of meters below the sea-surface, at high speeds in murky waters. Most of our inferences come from indirect observations or devices measuring depth, speed, and duration of dive, size of foraging group, stomach samples, and fish behavior.

Being flightless, *Spheniscus* penguins must encounter frequent, inshore food sources, as the birds must swim, not fly, to their foraging grounds and underwater searching visibilities are short (Frost et al., 1986a). Penguins seem to travel directly, often in groups (e.g. Siegfried et al., 1975; Boersma, 1977; Broni, 1986) to a certain area, then begin searching (e.g. Wilson and Wilson, 1988; Heath and Randall, 1989). We do not know whether physical (e.g. depth, bottom topography, currents, wave height, temperature) or biological (turbidity, presence of fish schools) clues lead the birds to stop traveling and start searching, by diving. Locating the school at a fishing area may be done by an individual bird, or it may be attracted to calls by other penguins (Broni, 1986) or by foraging by other species (Duffy, 1983, 1989).

Most dives are relatively shallow (Wilson, 1985b), suggesting feeding on fish schools near the surface. Most penguin prey form schools and, while this may facilitate locating fish, penguins may find it difficult to target a single fish, amongst tens or hundreds of thousands of similarly-sized, similarly behaving fish. Based on bite marks on fish, penguins attack from below, perhaps silhouetting the fish against the surface (Wilson and Duffy, 1986; Wilson et al., 1989a) and using their dark dorsal plumage as camouflage (Cairns, 1986). They may also use the alternating black and white of the breast band as an aggressive display, herding the fish in a school closer and closer, until the minimum distance between fish breaks down and the school structure collapses (Wilson et al., 1987). Penguins may also use group fishing to break up school structure (Summer, continued from page 13
1934; Boersma, 1977; Boswall and MacIvor, 1975; Wilson et al., 1987) or may join with other predators that effectively serve the same role (Boersma, 1977; Broni, 1986), although Wilson (1985b) suggests that African Penguins forage on smaller schools of fish than do other birds. Finally, penguins may drive fish to the surface for other, more shallowly-diving birds (Broni, 1986).

Contributions From Captive Studies

Those who have an opportunity to study the Spheniscus Penguins in captivity have much to contribute to our basic knowledge and research that will aid in penguin conservation. Such research can range from the intensive, such as behavioral studies, to low-key, such as consistent measurements of mass and body measurement of individual penguins over time.

Careful measurements of several generations of penguins, raised under constant conditions, will give us a much-needed idea of heritability of body size. If we can measure the relative contributions of environmental and genetic factors, we can perhaps use changes in body size to monitor population dynamics of Spheniscus penguins (Duffy, 1987b). This will be invaluable in examining the possible effects of competition with commercial fisheries and of climate change. Measurement of known genetic lineages can also give us some idea of the genetic basis for partial and complete double breast banding in African and Humboldt penguins and can be compared with molecular genetic studies.

We know something about the courtship and mating behavior of two of the species (e.g. Boersma, 1977; Eggleton and Siegfried, 1979), but we have little information about Humboldts or Magellanes (Jouventin, 1982). It would be extremely useful to have basic ethograms of the four species, to allow comparison of their species-specific and sex-specific behaviors in captivity (e.g. Merritt and King, 1987; Scholten, 1989). Adding or removing breast bands would be an interesting experiment to test the importance of such coloration between species (cf. Ryan et al., 1987). It would also be interesting, without allowing actual reproduction, to study the behavior of mixed-species pairs in captivity.

Work on aging and sexing penguins is extremely important and useful (e.g. Cooper, 1972; Bulfon et al., 1986; Boersma and Davies, 1987; Scolaro, 1987a; Scolaro et al., 1983). Measurements of captive birds, under constant conditions, over time will greatly aid field studies (e.g. Edgington, 1989). Determination of the growth of young (Cooper, 1977), energetics (Erasmus and Smith, 1974), and of age of first-breeding under controlled, captive conditions would also be very useful for comparison with similar measurements made in the much more variable natural conditions.

Birds, such as those kept at Sea World, Inc. in Mission Bay, San Diego, may potentially play an important role in our understanding of how penguins detect El Niño. Linda Henry and I have been examining data that seem to show that the Humboldt Penguins at Sea World stopped breeding during the severe 1983 El Niño. These birds were fed ad libitum, so food shortage was not responsible. What clues caused them to stop (cf. Merritt and King, 1987)?

Finally, the development of inexpensive, safe artificial burrows and their testing in captivity would provide a useful management tool for penguin managers in the field. For example, lack of sites on small islets may force penguins in Africa and Galapagos to nest on the mainland or on larger islands where they are vulnerable to terrestrial predators. Artificial burrows could raise the 'carrying capacity' of such sites.

Conclusion

This is a highly condensed review of the literature on field studies of Spheniscus penguins. It does not, for lack of space, do justice to many fine studies and to the physical environments in which the birds nest and forage or to the ecology of prey species. We know a great deal about Spheniscus penguins, especially their nesting ecologies and diets, but, even with the development of increasingly sophisticated means of studying penguins at sea, we are really only beginning to understand the marine part of their existence. Unfortunately, field researchers can be criticized, with a few bright exceptions, for not applying our knowledge to the management and conservation of Spheniscus penguins. The managers of captive penguins with their direct management experience, albeit at a very small scale, can play an important role in applying the insights of field work to the management of wild, as well as captive populations.

References are included in the bibliography which follows.
A Selected Bibliography of the Spheniscus Penguins

David Cameron Duffy

I have attempted to make this bibliography as complete as possible and it probably contains most of the more important Spheniscus ecology papers published before 1987. Historical, local colony counts and more recent papers, especially those in regional journals, may have been omitted. I would appreciate references or reprints of missing recent papers.


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