IRIS COLOUR OF HUMBOLDT PENGUINS *SPHENISCUS HUMBOLDTI*

C.J. SCHOLTEN

Boersterweg 14, 9791 HE Ten Boer, The Netherlands
(t.van.de.gronde@oprit.rug.nl)

SUMMARY

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From 1983–1996, the iris colour of 45 to 65 captive Humboldt Penguins *Spheniscus humboldti* at Emmen Zoo, The Netherlands, was monitored monthly. As chicks and juveniles, Humboldt Penguins at first have dark (grey) irides, which become pale after a while. In most adults the pale irides eventually become red, but some individuals continue having pale irides. Males attain red irides at an earlier age than do females. Two very old males were found to have black irides. In winters on average a slightly redder iris than in the following summer was observed. Iris colour between and within penguin species is darker at higher latitudes. Possible explanations for this are discussed.

INTRODUCTION

Iris colour varies greatly between bird species, but also within species (Bond 1919, Hardy 1973) and within individuals (Bond 1919, George 1972, Trauger 1974, Manuwal 1978, Picozzi 1981, Newton & Marquiss 1982, Nelson 1983, Sweijd & Craig 1991). The function of iris colour is thought to be either part of the animal's display plumage or contributing towards the cryptic colouration of the bird (Martin 1985).

In some species relationships between iris colour and age, sex or breeding season have been found. A relationship between iris colour and age has been established in European Sparrowhawks *Accipiter nisus* (Newton & Marquiss 1982), in Cassin's Auklets *Ptychoramphus aleuticus* (Manuwal 1978) and in African Pied Starlings *Spreo bicolor* (Sweijd & Craig 1991). Relationships between iris colour and sex have been established for the Golden Pheasant *Chrysolophus pictus* (Bond 1919) and San Blas Jay *Cyanocorax sanblasiana* (Hardy 1973). Sex-related differences in age at which iris colour is attained have been shown for *Accipiter* species (Newton & Marquiss 1982), Hen Harrier *Circus cyaneus* (Picozzi 1981), Lesser Scaup *Aythya affinis* (Trauger 1974) and Common Goldeneye *Bucephala clangula americana* (Nelson 1983). A relation between iris colour and breeding status has been found in the Armenian Gull *Larus argentatus armenicus* (Filchagov 1993). Sometimes such findings have been incorrectly extrapolated to other species. However, it is necessary to investigate factors influencing iris colour for individual species.

When attempting to identify and sex captive Humboldt Penguins *Spheniscus humboldti* without handling them my attention was drawn to their iris colour, because, as noted by Murphy (1936) for wild birds, there was great variation between individuals. Because factors regulating iris colour were not immediately obvious, iris colour of individual birds was monitored over a long period to determine mechanisms controlling it.

METHODS

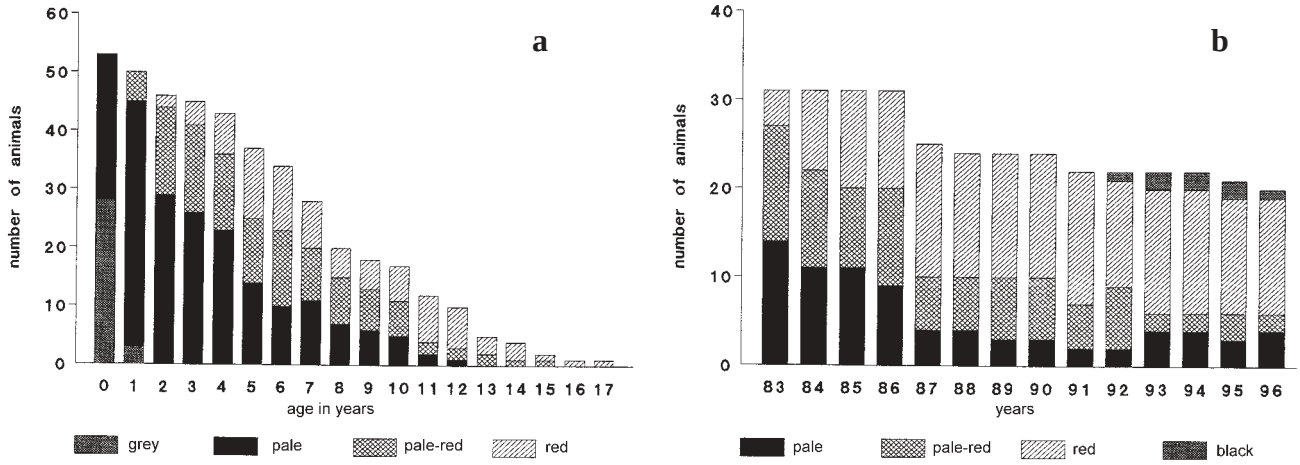
The data analysed in this paper were collected in a captive colony of Humboldt Penguins in Emmen Zoo, The Netherlands from March 1983 to March 1996. During the study period the colony consisted of 45 to 65 birds. The colony included adults caught in the wild in 1976 and in 1978. In March 1983 there were 30 wild-bred and 15 zoo-bred birds, and in March 1996 17 wild-bred and 29 zoo-bred birds. In December 1983, the penguins underwent cloacal examination to determine sex. The sex of some birds was determined on behavioural grounds (Scholten 1987) and others after death. Individuals were recognized on the basis of the pattern of spots on their breast (Scholten 1989). Chicks were banded until they acquired a distinctive breast pattern.

Throughout the study period, iris colour for each individual was determined monthly by the same person using binoculars. The colour descriptions used were: grey, pale, pale red, red, black and their intermediates. The Munsell system of colour notation divides colour into three components: hue (redness), value (black/white) and chroma (intensity of hue) (Wood & Wood 1972). In this study for the classes pale, pale red and red, only the amount of redness (comparable to the'hue') was recorded and not the black/white component.

For purposes of analysis colour classes were coded (Table 1). Iris colour was determined for either the left or right eye, whichever was most visible at the time. On a few occasions, a colour difference between eyes was noticed, but this was only temporary.

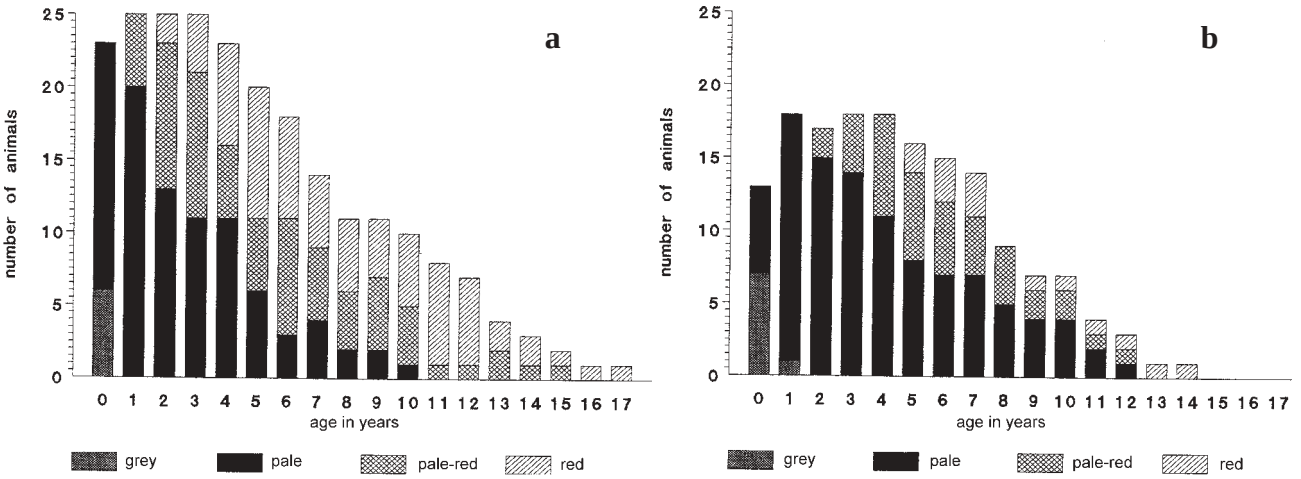
RESULTS

Age-related differences in iris colour for both sexes combined for birds of known age are shown in Figure 1a. Statistically, iris colour was strongly age-related ($P < 0.0001$). The majority of zoo-bred penguins had grey irides during their first year (age 01, Fig. 1a). At ages between one and four years, the majority of animals had pale irides. Most older birds had pale red or red irides. The youngest animals with pale-red and red eyes were one and two years of age, respectively. The oldest zoo-bred penguin that had a pale iris during the study was 12 years of age.



Analysis of covariance (mixed model): Age: $P < 0.0001$

Fig. 1. *Iris colour in Humboldt Penguins of known age (a) and in an ageing population of wild-bred birds that were all in adult plumage in 1978 (b).*



Analysis of covariance (mixed model): Age: $P < 0.0001$; Sex: $P = 0.0665$; Age*sex: $P = 0.5614$

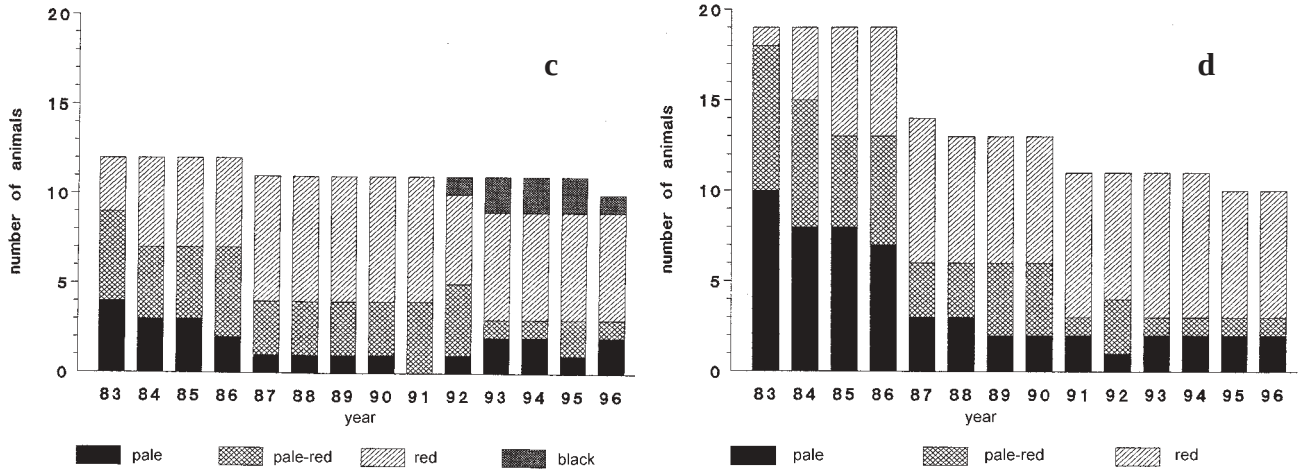


Fig. 2. *Iris colour in Humboldt Penguins of known sex – (a) males of known age, (b) females of known age, (c) wild-bred males, (d) wild-bred females.*

For the wild-bred birds, age could not be determined since they were adults on arrival at the zoo in 1976 and 1978. In 1983 they must therefore have been at least seven to nine years of age, since Humboldt Penguins attain adult plumage after approximately one year (7–19 months, Figs 4a & b). After 1978, no wild-bred birds were added to this group, so their average age increased over the years until birds started to die. Statistically, iris colour of wild-bred birds was strongly correlated with years ($P < 0.0001$, Fig. 1b). Until 1987 the trend in wild-bred and zoo-bred animals was similar. The number of birds with pale irides decreased with increasing age, whereas the number of animals with red irides increased. After 1987, the number of wild-bred birds with pale irides stabilized. In 1996, there were still a few wild-bred birds with pale irides and they must have been at that time at least 19–21 years old. From 1992, there were two individuals (males) with black irides. It was clear that these were very old animals, since they had a lot of horn around the bill. Both animals have since died.

Both males and females can have grey, pale or red irides (Figs 2a–2d). However, black irides were only found in males. Males generally had a higher value for iris colour than did females ($P = 0.0665$). Females seemed to attain certain colours at a later age than males did. Males had grey irides only during their first year (age 0), but some females had grey irides during their second year (age 1). Some males had pale red irides at age one, but no females attained pale red irides until age two. The greatest difference was found in red irides, which some males attained at age two but females only from age five.

The majority of Humboldt Penguins scored grey irides until about six to seven months old (Fig 3). After that the number of pale irides increased rapily. Pale red irides were found for the first time at 13 months of age and red irides at 17 months of age.

Grey irides were mainly restricted to birds in juvenile plumage (Figs 4a & b). Only once was a bird in adult plumage scored with a grey iris. The opposite was true for pale red and red irises. Only one bird in juvenile plumage was scored once with a pale red iris. All other animals under two years of age with pale red or red irises were in adult plumage.

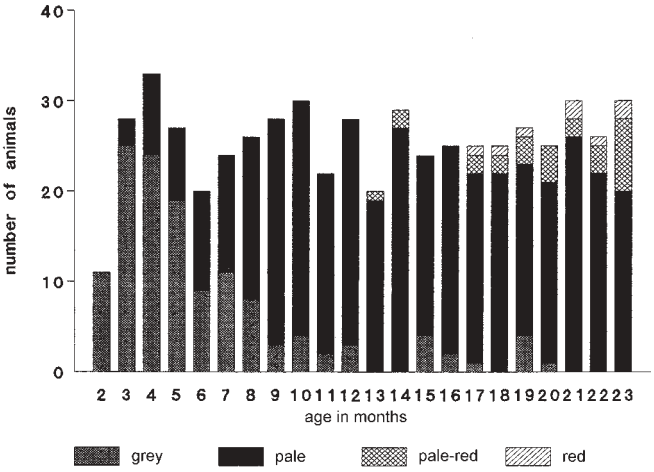
In eight out of 12 comparisons winter values for iris colour were higher than those in the following summer ($P = 0.049$, Fig. 5). Because iris colour is strongly age related, the opposite

TABLE 1

Codes allocated to iris colours of Humboldt Penguins

Iris colour	Value	Iris colour averages
Grey	10	0 – 24.99
Grey/pale	20	
Pale	30	25 – 44.99
Pale (red)	40	
Pale red	50	45 – 64.99
Red (pale)	60	
Red	70	65 – 79.99
Black	80	80

For Figures 1 to 4 iris colour averages of individuals were reduced to five classes.



Analysis of covariance (mixed model): Age: $P < 0.0001$; Sex: $P = 0.6619$; Age*sex: $P = 0.2820$

Fig. 3. *Iris colour in Humboldt Penguins (sexes combined) during their first two years of life.*

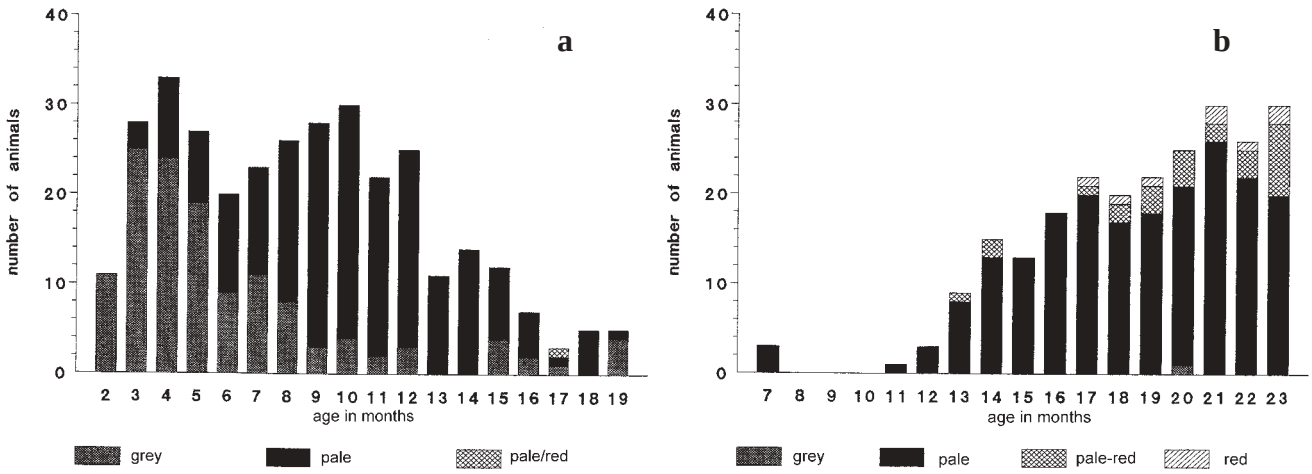
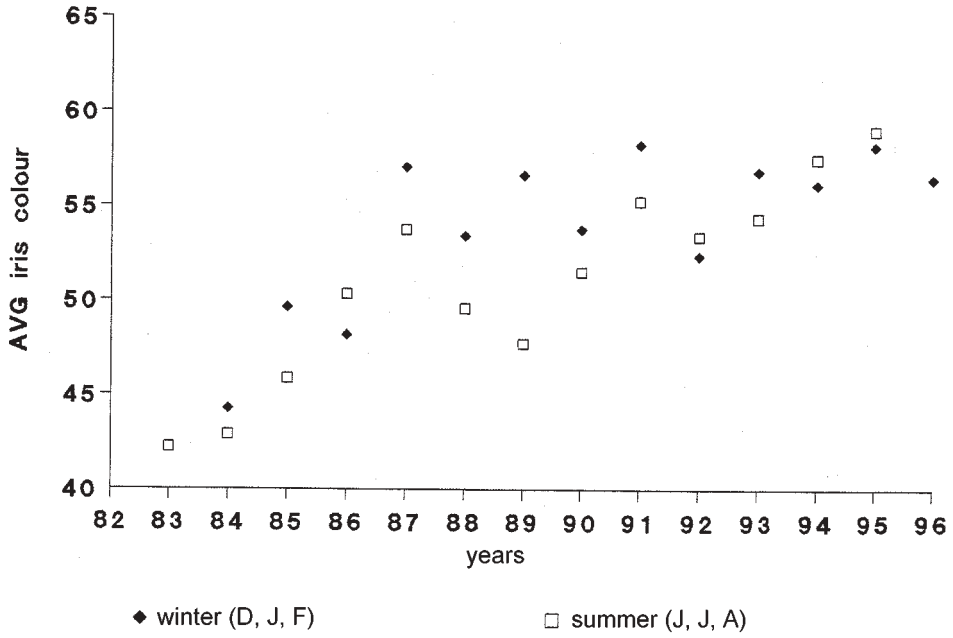


Fig. 4. *Iris colour in Humboldt Penguins (both sexes combined) under two years of age having (a) juvenile and (b) adult plumage.*



Analysis of covariance (mixed model): Age: $P < 0.0001$; Sex: $P = 0.0619$; Season: $P = 0.0490$; Age*sex: $P = 0.2820$

Fig. 5. *The average value of iris colour in winter (December to February) compared with that in the following summer (June to August).*

would have been expected, since in general the value of average iris colour increased as age increased.

DISCUSSION

Iris colour in Humboldt Penguins

Humboldt Penguins can have various iris colours. Both males and females can have grey, pale, pale red, and red irides. Black irides were only found in two old males.

A dark juvenile iris seems to be achieved in two ways. In the African Pied Starling *Spreo bicolor* (Sweijd & Craig 1991) the anterior border layer of the juvenile (dark brown) iris is darkly pigmented as it is in the Herring Gull *Larus argentatus* (Bond 1919) In the adult (white) iris this layer is replaced by reflecting pigment granules. Andrew & Naik (1965) found in nestling Jungle Babblers *Turdoides striatus* that the dark colour was caused by a dark pigmented epithelium, which was visible through the thin transparant muscle layer and stroma. In older birds more numerous muscle fibers made the iris opaque and cream coloured. The pigmented epithelium was found by Oehme (1969) to contain melanin in all 140 species he examined.

According to Bond (1919) the red colour in irides of birds is achieved in two ways. The ruby colour can be a superimposition effect due to the covering of red blood vessels with yellow pigment cells (doves and pigeons) or is due to the presence of cells packed with fine granules of a reddish-mauve coloured pigment (Cayenne Lapwing *Vanellus cayennensis*). In the first case the ruby colour fades after death, in the second the colour persists.

In this study grey (dark) irides were restricted to the chick and juvenile stages. All individuals attained pale irides before the end of their second year. Pale red and red irides were restricted to the adult stage. In Hen Harriers, a change to a yellow iris (nestlings have grey-brown irides) in males coincided with their assumption of adult plumage, whereas in females, which exhibit no distinctive plumage change with age, the iris took six or more years to change to yellow (Picozzi 1981). That males change iris colour at an earlier age than females has been observed for other species of birds, such as *Accipiter* hawks (Newton & Marquiss 1982), Hen Harrier (Picozzi 1981), Lesser Scaup (Trauger 1974) and Common Goldeneye (Nelson 1983).

In this study, not all adults attained red irides, and those that did showed great variation in the age at which the different colour stages were reached. Therefore, in Humboldt Penguins iris colour alone is unsuitable for precisely determining age of adult birds, as it is in Sparrowhawks (Newton & Marquiss 1982) and in Cassin's Auklets (Manuwal 1978).

Factors such as maturity stage, age and sex, found in this study to correlate with iris colour, fit the theory that iris colour is under hormonal control (androgens) (Trauger 1974).

Seasonal differences in iris colour have been found in several bird species, the iris being darker in winter than in the breeding season (e.g. Armenian Gull, Filchagov 1993). The seasonal differences found in this study were not great and cannot be described as changing from red to yellow as recorded for the Rockhopper Penguin *Eudyptes chrysocome* (Duke-Elder 1964). The possibility of the observed seasonal differences being due to observer error caused by different light in winter and summer is unlikely, since in my experience more light (summer) shifts the colour observation towards red, so that a higher rather than a lower colour value is recorded.

Iris colour in penguin species

It seems that the sequence of colour phases in irides of Humboldt Penguins (dark to pale to red to black) also occurs in other species of penguin. As chicks they have dark irides,

which then get pale or slightly paler before becoming red or red-brown (Table 2). It is the timing of these changes, and the phase where the process stops, that varies greatly from species to species. The adult (final) iris colour varies from pale (or yellow) in the Little Penguin *Eudyptula minor* and Yellow-eyed Penguin *Megadyptes antipodes* to dark brown in the *Aptenodytes* genus (Table 3).

At the level of genus there is suggestion that the phylogenetic trends in penguins described by Jouventin (1982) are consistent with the extent to which the adult iris is reddish brown. The phylogenetic trends are related to latitude (Jouventin 1982). Possibly colour of irides is also related to latitude.

Within some genera, the above trend seems also to be true. In *Pygoscelis* the Adélie Penguin *P. adeliae* lives at a more southerly latitude than do Chinstrap *P. antarctica* and Gentoo *P. papua* Penguins (Jouventin 1982) and has to a greater extent very dark brown irides (Table 3). Within the *Spheniscus* genus the African Penguin *S. demersus* and the Magellanic Penguin *S. magellanicus* have darker irides than the lower-latitude Humboldt and Galapagos *S. mendiculus* Penguins.

Higher latitudes have lower temperatures. In general dark colours absorb more radiant energy than do light colours, and are thus expected to be more frequent in colder climates (Savalli 1995). The maximum angle between sun and horizon, and thus light composition, also varies with latitude. This might prove to be important for a light-sensitive organ like the eye. Pigments can provide, for example, protection. Melanin (and carotenoids) protect the eye from UV radiation (Savalli 1995). The amount to which animals are exposed to UV radia-

TABLE 2

The iris colour of chicks and juvenile penguin species, ordered from pale to dark

Species	Iris colour		Reference number	Video number
	Chick	Juvenile		
Little Penguin *Eudyptula minor*	dark	pale	33	12
Yellow-eyed Penguin *Megadyptes antipodes*	dark (brown)		7, 30	15
Galapagos Penguin *Spheniscus mendiculus*		dark (–pale?)	3	
Humboldt Penguin *S. humboldti*	dark (grey)	dark-pale	pers. obs.	
African Penguin *S. demersus*		pale-red-brown	pers. obs.	
Magellanic Penguin *S. magellanicus*		dark	14, 22	18
Rockhopper Penguin *Eudyptes chrysocome*	dark-red	dark-red		21, 22
Fiordland Crested Penguin *E. pachyrhynchus*				
Snares Crested Penguin *E. robustus*		grey-brown	44	
Royal Penguin *E. schlegeli*	dark	dark		16
Macaroni Penguin *E. chrysolophus*				*7*
Erect Crested Penguin *E. sclateri*				
Chinstrap Penguin *Pygoscelis antarctica*	dark (grey)	dark-pale	7, 20, 30, 25, 46	18
Gentoo Penguin *P. papua*	dark (grey)		6, 7, 21, 30, 37	
Adélie Penguin *P. adeliae*	dark (grey/brown)	dark-pale (brown)	1, 4, 20, 50	1, 6, 11, 13, 16, 22
King Penguin *Aptenodytes patagonicus*	dark (-light) brown		15, 20, 22	14, 17, 19
Emperor Penguin *A. forsteri*	dark (black)		7, 25	4, 8, 10

TABLE 3

The iris colour of adult penguin species ordered from pale to dark

Species	Iris colour*	Reference number	Video number
Little Penguin *Eudyptula minor*	PALE	pers. obs., 7, 9, 30, 33, 37, 42, 48, 50	12
Yellow-eyed Penguin *Megadyptes antipodes*	PALE	7, 30, 48, 50	15, 16
Galapagos Penguin *Spheniscus mendiculus*	(pale?)-red-dark (brown)	3, 7, 15, 28, 37, 55	5
Humboldt Penguin *S. humboldti*	PALE RED-dark	pers. obs., 28, 37, 50	
African Penguin *S. demersus*	(pale)-red-BROWN	pers. obs., 7, 8, 37	
Magellanic Penguin *S. magellanicus*	red-DARK (brown)	pers. obs., 9, 14, 20, 22, 28, 37, 43, 50	3, 22, 23
Rockhopper Penguin *Eudyptes chrysocome*	RED	pers. obs., 4, 7, 9, 14, 18, 26, 37, 46, 47, 48, 54	17, 21
Fiordland Crested Penguin *E. pachyrhynchus*	RED-dark (brown)	37, 48, 50, 54	
Snares Crested Penguin *E. robustus*	red-reddish brown	35, 44, 52	
Royal Penguin *E. schlegeli*	red	7, 18, 20, 30, 37	16
Macaroni Penguin *E. chrysolophus*	red-REDDISH BROWN-brown	1, 4, 7, 15, 18, 20, 30, 37, 55	7, 9
Erect Crested Penguin *E. sclateri*	reddish brown-BROWN	12, 37, 45, 50, 53, 54	22
Chinstrap Penguin *Pygoscelis antarctica*	red-REDDISH BROWN-brown	1, 7, 15, 18, 20, 21, 25, 26, 30, 37, 46, 55	
Gentoo Penguin *P. papua*	(red)-reddish brown-DARK (BROWN)	1, 4, 7, 18, 26, 36, 37, 48	20, 21
Adélie Penguin *P. adeliae*	DARK (BROWN)	18, 20, 37, 50, 55	1, 2, 6, 8, 13, 16
King Penguin *Aptenodytes patagonicus*	DARK (BROWN)	pers. obs., 1, 4, 7, 17, 18, 20, 26, 27, 37	14, 16, 17
Emperor Penguin *A. forsteri*	DARK (BROWN)	7, 15, 25	4, 8, 10, 16

*Capitals denote the colour most commonly observed.

tion should therefore be considered. There is a theory predicting that species living in wide open spaces have darker irides than those living in more enclosed environments (Savalli 1995).

For unravelling the mechanisms involved in producing iris colour in penguins, more research will be needed on iris colour of other penguin species at different localities and latitudes and on the pigments involved in producing iris colour.

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6. Ja Natuurlijk Extra: De Keizerspinguin. Producer: Warren, A. Production: BBC.
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8. Keizerspinguins van de Zuidpool. 1992. Producer: Harraway, N. Production: Nat. Hist. Unit Tel. New Zealand & Discovery Product./ Rai 3.
9. Life in the freezer: South Georgia. 1993. Producer: Fothergill, A. Production: BBC/Nat.Geogr. Soc./ Lion Heart Tel Int. Inc.
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11. Lilliput in Antarctica. 1990. Production: The Cousteau Society, Inc.
12. Little Penguin. 1987. Production: Manners/ Wreford – Reed Pr. Austr./ Phill. Isl. Peng. Res.
13. Lorne's Greene New Wilderness: Adelie Penguins. 1983. Producers: Greene, Ch. & Dewar, S.W. Production: Greene & Dewar New Wilderness prod./ CTV Tel. Network.
14. Macquarie Island. Producer: Parer, D.
15. Nieuw-Zeeland's vreemde vogels.
16. Penguin Summer. Producer: Mauakami, K. Production: Thomas Horton Ass.Ventura. USA.
17. Rockies and Rollers. Production: BBC TV / National Geographical Society.
18. Search for Adventure: Antarctic Challenge. 1990. Producer: Horton, T.F. Production: Colstar-Thomas Horton Ass./ ATBF-Liege – Belgium.
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20. The World of Nat. Geographic: Voyager: Het Antarctisch Avontuur.
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